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Vol. 75, No. 4 October 1977

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Seattle, Washington

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Fishery Bulletin

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LIFE HISTORY, FEEDING HABITS, AND FUNCTIONAL MORPHOLOGY OF JUVENILE SCIAENID FISHES IN THE YORK RIVER ESTUARY, VIRGINIA[1,2]

LABBISH N. CHAO[3] AND JOHN A. MUSICK[4]

ABSTRACT

Four abundant sciaenid fishes, *Cynoscion regalis*, *Bairdiella chrysoura*, *Micropogonias undulatus*, and *Leiostomus xanthurus*, use the York River, Va., as a nursery ground and as an adult seasonal feeding ground. In addition, six species of sciaenids, *Menticirrhus saxatilis*, *M. americanus*, *Sciaenops ocellata*, *Cynoscion nebulosus*, *Pogonias cromis*, and *Larimus fasciatus*, are present in the estuary occasionally. Yearling *C. regalis* were first caught in April and young-of-the-year in July or August. Yearling *B. chrysoura* were first caught in March or April and young-of-the-year in July or August. Juvenile *Micropogonias undulatus* and *Leiostomus xanthurus* may be present in the York River all year-round. Young-of-the-year *L. xanthurus* were first caught in April and *M. undulatus* were first caught in August. Small *M. undulatus* (<20 mm TL) were caught from August to June, which may indicate a prolonged spawning season (or a late spawning stock). Emigration to the ocean was found in all the four species during late fall or early winter. Water temperature and dissolved oxygen seemed to be the most important factors in the spatial and temporal distributions of these four species in the York River.

Mouth position, dentition, gill rakers, digestive tract, pores and barbels, nares, and body shape of six sciaenid species, *Larimus fasciatus*, *C. regalis*, *B. chrysoura*, *M. undulatus*, *Menticirrhus saxatilis*, and *Leiostomus xanthurus*, were found to be important in locating and ingesting prey in the water column. Stomach contents indicated that the food partitioning of these six species was closely correlated with the species and their prey habitat. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* fed mainly above the bottom, whereas *Micropogonias undulatus*, *Menticirrhus saxatilis*, and *L. xanthurus* fed on epifauna, infauna, or both. Juvenile sciaenids are able to coexist in the same area because of differences in spatial and temporal distribution, relative abundance, and food habits.

Sciaenid fishes are among the most important inshore bottom fishery resources of the Atlantic and Gulf of Mexico coasts of the United States (Roithmayr 1965; Joseph 1972; Gutherz et al. 1975). Sciaenid fishes usually use the estuary as a nursery ground and seasonal feeding ground. Among the 14 species of sciaenids recorded from Chesapeake Bay proper (Musick 1972), young-of-the-year of 10 species were caught in the York River system during this study. *Leiostomus xanthurus*, *Micropogonias undulatus*, *Bairdiella chrysoura*, and *Cynoscion regalis* were the most abundant species. *Menticirrhus saxatilis*, *M. americanus*, *Sciaenops ocellata*, *C. nebulosus*, *Pogonias cromis*, and *Larimus fasciatus* were caught only occasionally.

Juvenile sciaenids, except the Atlantic croaker, *Micropogonias undulatus*, usually entered the York River in late spring and left in late fall. During this period, sciaenid fishes dominated bottom trawl catches in the York River (Colvocoresses 1975; Markle 1976). By yearly average, they composed more than 50% of the total catch by weight and 18 to 28% by number of individuals. The purpose of this study is to describe the coexistence of the four most abundant juvenile sciaenids in the York River system, Va., based upon relative abundance, temporal and spatial distribution, length frequency, apparent movements, and feeding habits. Morphological structures related to feeding habits and habitats were also studied. Specimens of the banded drum, *Larimus fasciatus*, and the northern kingfish, *Menticirrhus saxatilis*, were included to show the range of variability in the feeding habits of juvenile sciaenids. Bottom trawl surveys conducted by the Virginia Institute of Marine Science (VIMS) from January 1972 to

[1]A portion of a dissertation submitted to the School of Marine Science, College of William and Mary, Williamsburg, Va., in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science, by the first author, May 1976.

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December 1974 provided the data for analyses of distribution and food habits. An analysis of fish community structure based on this data has been reported by Colvocoresses (1975).

The York River and its major tributaries (Pamunkey and Mattaponi rivers) represent an estuarine system which is relatively well known biologically and is relatively undisturbed (Boesch 1971). The general trend of geomorphology, hydrography (salinity, dissolved oxygen, and temperature), ecology, and alteration by man of the area were described by McHugh (1967), Boesch (1971), and Brehmer.[5]

MATERIALS AND METHODS

Survey Programs

Seven longitudinal strata (A, B, C, D, E, F, and G) and three cross-sectional substrata (north shoal, channel, and south shoal) within each stratum were sampled monthly (Figure 1). Shoal hauls were usually in water <4 m and channel hauls in water >5 m deep. Randomly numbered square grids (540 m on a side) were assigned as trawl stations. In the lower 16 km (10 miles) of the York River, strata A, B, C, and D were sampled from March 1972 to December 1974. The upper part of the York River was sampled from January 1972 to March 1974, but the random method was not used until June 1972 and strata E, F, and G were not designated until January 1973. Before the random sampling program, fixed sampling stations in the channel were assigned at 8-km (5-mi) intervals from the mouth of the York River (mile zero) up to 45 km (mile 28, also see Haven 1957; Markle 1976). Data from fixed station samples (January–May 1972) were combined within the strata for analyses. Lower portions of the Mattaponi and Pamunkey rivers (strata: M and P) were sampled after January 1973. Three substrata (1, 2, and 3) were set at 8-km (5-mi) intervals for the lower 24 km (15 mi) upstream from their confluence with the York River (about 45 km from the York River mouth). Each sampling stratum was divided into station grids, each measuring 540 m on a side; four to six grid stations were sampled randomly from each stratum monthly.

Gear

Bottom trawl tows were against the current, of 5-min duration on the bottom with a 4.9-m (16-ft) semiballoon otter trawl (7-m rope, 1.9-cm bar mesh, 0.63-cm bar mesh cod end liner), 7-m bridle, and 0.6-m weighted otter doors at a speed of approximately 90 m/min. Nine stations were sampled monthly with beach seines along the shores of lower parts (strata A–D) of the York River (Figure 1) and three replicate hauls were made with a 15.25-m (50-ft) bag seine (1.8 m deep with a square bag, 0.64-cm bar mesh in the wing and 0.48-cm bar mesh in the bag). Thirteen beach seine stations were selected along the shores of the upper part of the York River (strata E–G, Figure 1). These stations were only sampled from July to October in 1972 and 1973 with a 30.5-m (100-ft) bag seine. Beach seine data were used only for length frequency analysis in the present study. Hydrographic (salinity, temperature, and dissolved oxygen) data were collected from both surface and bottom water.

Sampling Procedure

All fishes were identified, counted, and weighed in the field or laboratory. Total length (TL), measured from snout to the posterior tip of the caudal fin (on the midline), was taken to the nearest millimeter. All individuals of each species were measured from each trawl haul. For very large catches, at least 25 individuals were subsampled. Specimens were randomly selected for stomach analyses and preserved in 10% Formalin;[6] stomachs were dissected out and transferred to 40% isopropanol or 70% ethanol. Stomach contents were identified to the lowest practical taxon and frequency of occurrence of each item was recorded.

The standard methods of Hubbs and Lagler (1964) were used for all counts and measurements, if applicable. Upper and lower jaw lengths were measured from tips of the premaxilla and dentary, respectively, to the symphysis at the posterior corner of the mouth gape. Digestive tracts were removed from the fish. The intestine was straightened and measured from its junction with the stomach to the anus. Osteological observations

[5]Brehmer, M. L. 1970. Biological and chemical studies of Virginia's estuaries. Unpubl. manuscr., 120 p. Va. Inst. Mar. Sci., Gloucester Point.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

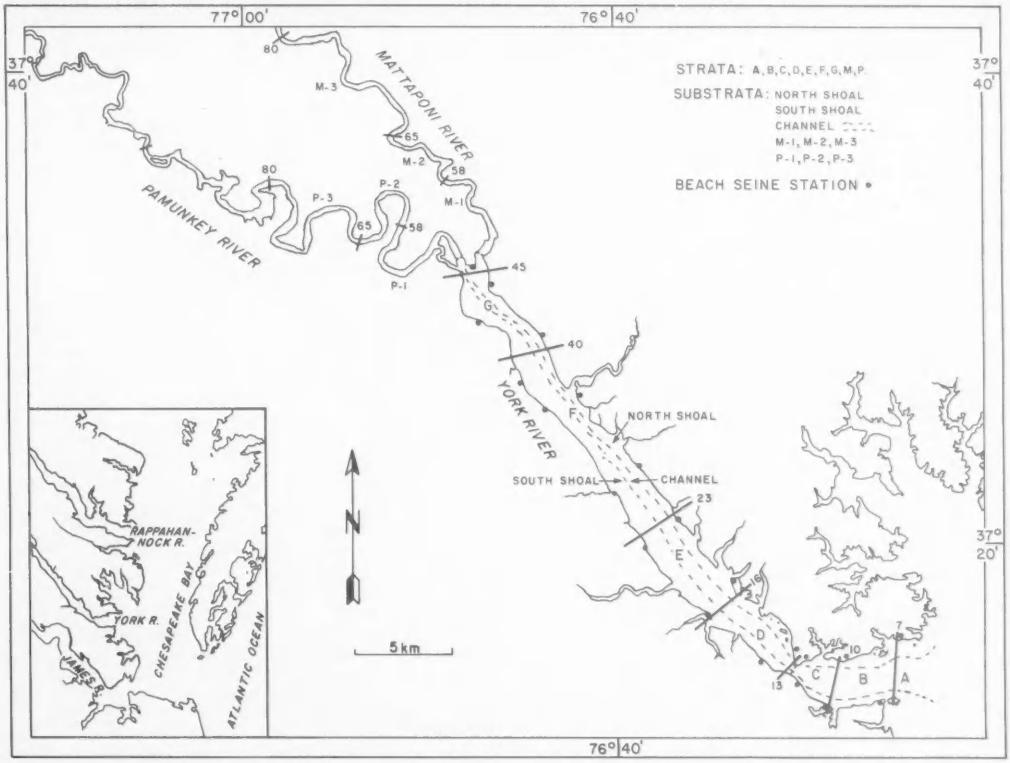


FIGURE 1.—The trawl strata, substrata, and beach seine stations in the York River estuary, Va. Strata: A–G, M, and P. Substrata: north shoal, channel, and south shoal. Substrata in Mattaponi River expressed as M-1, M-2, and M-3, in Pamunkey River as P-1, P-2, and P-3. River distances from the mouth of York River (0 km) are indicated in kilometers.

were made on cleared and stained specimens, according to the methodology of Taylor (1967).

The nomenclature used for the study fishes follows Chao (in press). *Micropogonias* must replace *Micropogon* because the generic name *Micropogon* was preoccupied by Boie (1826 in Aves). The specific name *chrysoura* is used instead of *chrysura* for *Bairdiella* because the spelling *chrysourus* was used by the original author (Lacepède 1803:166).

RESULTS AND DISCUSSION

Hydrographic Description

Water depth, temperature, salinity, and dissolved oxygen were measured with each sample and are listed in the appendix section of Chao (1976). The benthic environment was of particular importance to the present study. Mean values for bottom temperature, salinity, and dissolved oxygen in each stratum from May 1972 to August 1973 are summarized in Figure 2, to show seasonal patterns in the York River estuary.

Temperature

The bottom water temperature of the York River (Figure 2) was lowest in January and highest in July (1973) or August (1972). The gradual increase of temperature from April to June and the decrease from October to December are most important to migratory fishes in the York River (Markle 1976). In winter months (December–February), the bottom temperature of the upper portion of the York River was lower than that of the lower portion. No apparent differences in temperature were found among the shoal and the

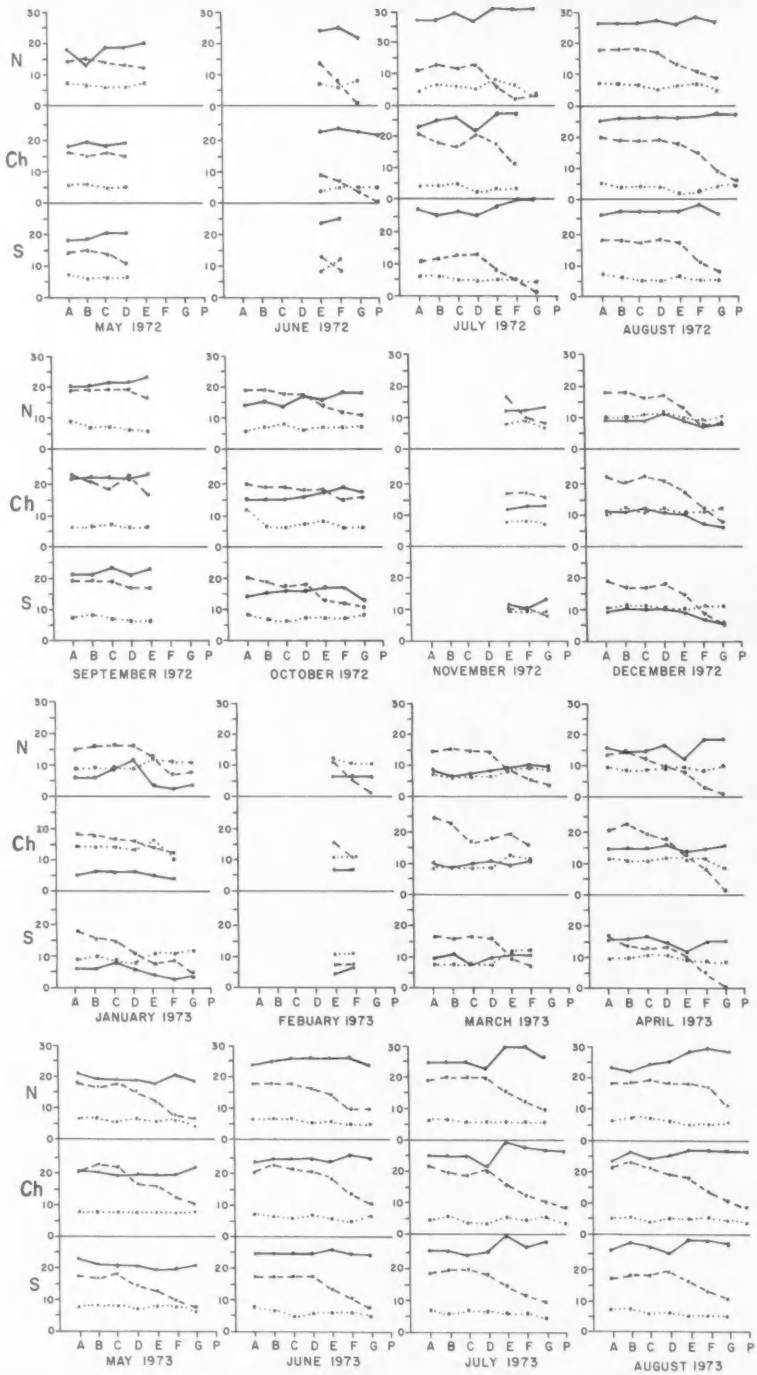


FIGURE 2.—Monthly means of the bottom temperature (°C—solid line), salinity (‰—dashed line), and dissolved oxygen (milligrams/liter—dotted line) in the York River estuary from May 1972 to August 1973. Strata: A–G in York River and P in Pamunkey River. Substrata: N = north shoal, Ch = channel and S = south shoal.

channel stations. In spring months (March–May), bottom temperatures increased rapidly, and the upper portion of the York River had slightly higher temperatures than the lower portion. The shoal stations also showed a slightly higher mean bottom temperature than the channel stations. In summer months (June–August), the bottom temperature of the upper portion of the river was higher than the lower portion. The shoal stations also showed a higher mean bottom temperature than the channel stations. In fall months (September–November), bottom temperature decreased rapidly. The upper portion of the river had slightly higher temperatures than the lower portion in the early fall (September–October). In early winter (December), bottom water temperature was slightly higher in the lower portion of the river (Figure 2). No apparent differences were found among the shoal and channel stations.

Dissolved Oxygen

Dissolved oxygen in the York River (Figure 2) was generally lower in warmer months (May–October) and higher in colder months (November–April). In the warmer months, dissolved oxygen was lowest at the deeper channel stations. There was no apparent difference between the upper and lower portions of the York River. In colder months, dissolved oxygen was slightly higher in the upper portion of the river and no apparent difference was found among shoal and channel stations.

Salinity

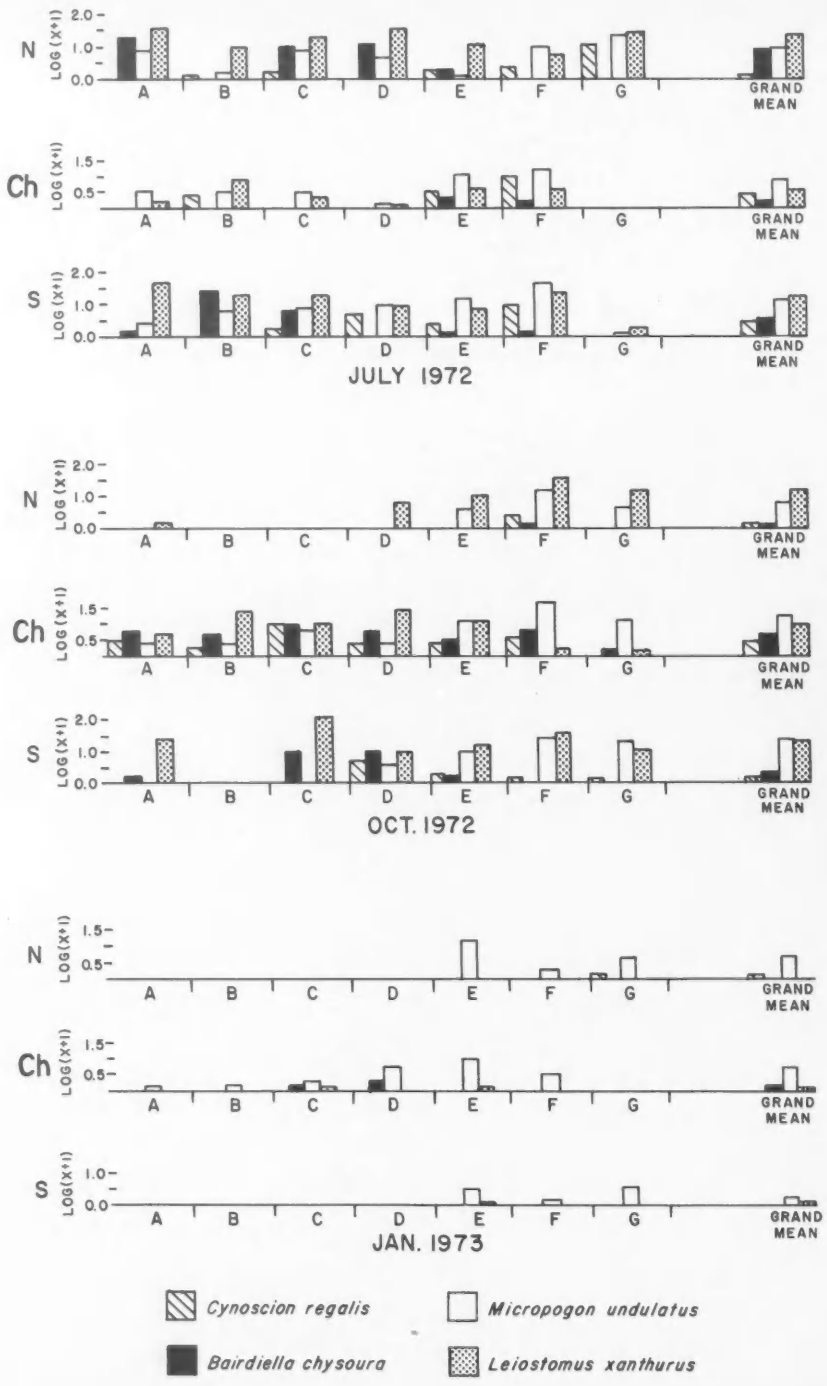
Salinity decreased toward the upper portion of the York River (Figure 2). Lower salinities usually were found in spring (March–May) and winter (December–February). The extremely low salinities of June to August 1972, were caused by hurricane Agnes (Anderson et al. 1973). Salinity at channel stations was usually higher than at shoal stations, especially in the lower portion of the river from March to June.

Temporal and Spatial Distributions

Young sciaenids are among the most abundant migratory finfishes in the York River (Massmann 1962; Colvocoresses 1975; Markle 1976). Temporal and spatial distributions of juveniles of the four most abundant sciaenids, *Cynoscion regalis*, *Bairdiella chrysoura*, *Micropogonias undulatus*, and *Leiostomus xanthurus*, are compared (Figures 3–5) to determine ecological partitioning during their estuarine life. The relative abundance of each species is expressed by the geometric mean, $\log_{10}(x + 1)$, of the individual catches per tow within the substrata, where x is the mean number of individuals per tow. Four months (July, October, January, and April) were selected to represent the seasonal abundances from different parts of the York River (Figure 3). Monthly mean catches per tow by river distance (stratum) and depth (substratum) were compared (Figures 3–5). Fishes caught in the Mattaponi and Pamunkey rivers were compared only by river distance (Figure 4).

In July 1972 and 1973, all four species of juvenile sciaenids were present in all parts of the estuary except the upper part (Figures 3–5). Relative abundance varied among species (Figure 3). *Bairdiella chrysoura* was more abundant in the lower and middle part of the river, while *C. regalis* and *M. undulatus* were more abundant in the upper part of the river (Figure 5). *Leiostomus xanthurus* was ubiquitous. *Micropogonias undulatus* gradually declined in abundance upstream in both the Mattaponi and Paumkey rivers (Figures 4, 5). *Leiostomus xanthurus* catches were quite variable in the Pamunkey River. This may have been caused by the contagious distribution of this species. Sciaenids were more abundant in shoal stations (Figure 3) than channel stations, especially in July 1972. Colvocoresses (1975) and Markle (1976) noted a general decline in the mean number of species and individuals of fishes caught per month in the summer from channel stations. This may be attributed to a reduction in the dissolved oxygen concentration, usually below 5 mg/l at the bottom of the channel (Markle 1976; Brehmer see footnote 5), and was apparently the case in the present study (Figure 2). Catches of *C. regalis* did not decline in channel stations, but this species is the best adapted for pelagic life of the four species studied (see "Correlation of Feeding Structures and Food Habits" section), and may have been captured in midwater where dissolved oxygen values did not decline.

In October (1972, 1973) juveniles of all four species of sciaenids were present in all parts of the estuary (Figure 3) and all reached their highest total abundance (Markle 1976). *Cynoscion regalis* was more abundant in the lower parts of the York River; *B. chrysoura* and *L. xanthurus* were more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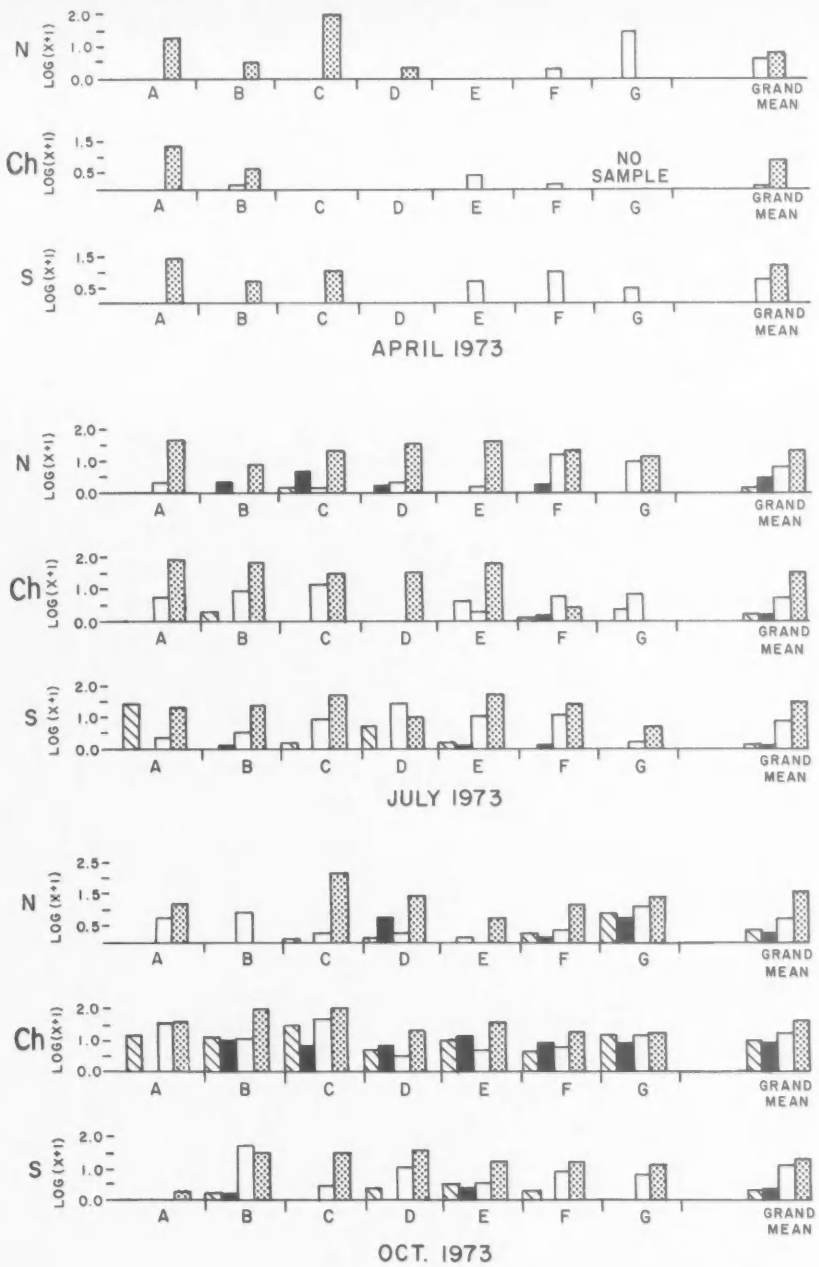


FIGURE 3.—Seasonal abundance of four juvenile sciaenids with depth and distance upstream in the York River. Mean numerical catch per tow of each substratum expressed as log $(x + 1)$. Strata: A–G; substrata: N = north shoal, Ch = channel, and S = south shoal.

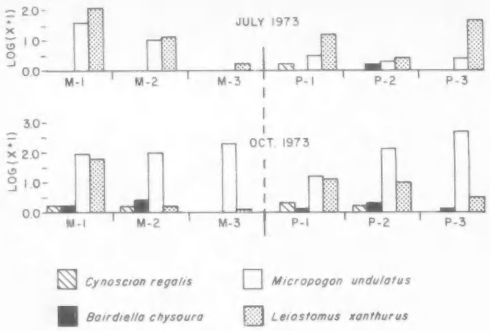


FIGURE 4.—Seasonal abundance of four juvenile sciaenids in the Mattaponi and Pamunkey rivers. Mean numerical catch per tow of each substratum expressed as log (x + 1). Strata: M = Mattaponi River, P = Pamunkey River. Substrata: 1, 2, and 3 designated by river distance upstream.

abundant in the middle part of the river. *Micropogonias undulatus* was more abundant in the upper part of the river, and especially in the Mattaponi and Pamunkey rivers (Figures 4, 5). Mean catch per tow increased up the estuary. Depth distribution of these four species of sciaenids indicated that they were more abundant in the channel stations (Figure 3). The relative abundance at south shoal stations was higher than at north shoal stations. The area was larger and the sampling depth was greater in the south shoal than the north shoal area (Colvocresses 1975; Chao 1976). Also, the average size of young sciaenids, especially the young-of-the-year groups, was larger in the channel than in the shoal stations (see section on "Distribution and Size"). Larger size juvenile sciaenids might use deeper areas to seek food and shelter.

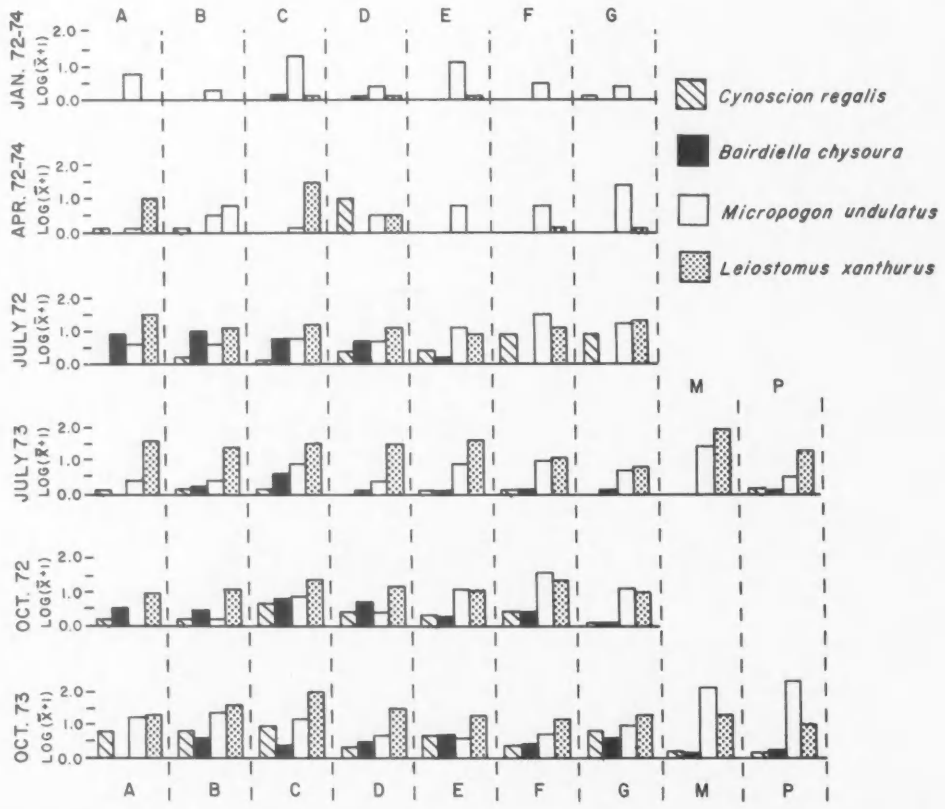


FIGURE 5.—Seasonal mean abundance of four juvenile sciaenids along the salinity gradient (strata) in the York River estuary. Grand mean numerical catch of four juvenile sciaenids per tow of stratum expressed as log (x + 1). Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Grand means of January and April represent the average of 3 yr. (1972 to 1974).

In January 1972–74, the numbers of individual sciaenid fishes were considerably reduced, except for *M. undulatus* (Figures 3, 5). *Cynoscion regalis, B. chrysoura,* and *L. xanthurus* were caught only occasionally. During the winter months, resident fish species were more abundant than transients, especially in the upper tributaries of the York River (Markle 1976). *Micropogonias undulatus* was the most abundant sciaenid fish in the middle part of the York River (Figure 5). Depth distribution in January 1973 (Figure 3), indicated that most fish were caught in the channel. Bottom temperatures of the channel stations were higher than shoal stations (Figure 2), which might have been the major factor causing the concentration of young sciaenids in the channel.

In April 1972–74, *C. regalis, M. undulatus,* and *L. xanthurus* were caught (Figures 3, 5). *Cynoscion regalis* was absent in 1973 (Figure 3) but sparse in 1972 and 1974 (Figure 5). *Micropogonias undulatus* was more abundant in the upper part of the river and *L. xanthurus* was more abundant in the lower reaches (Figures 4, 5), apparently because the young-of-the-year *L. xanthurus* had just entered the estuary (see section on "Distribution and Size"). Depth distribution of these two species (Figure 3) showed that they were more abundant in shoal areas, especially *M. undulatus. Bairdiella chrysoura* was completely absent.

Life History and Size

Length-frequency distributions (Figures 6–19) indicate that juvenile *Leiostomus xanthurus, Bairdiella chrysoura, Cynoscion regalis,* and *Micropogonias undulatus* enter the York River consecutively from April on, and all but *M. undulatus* leave the York River by December. Seasonal size distributions of these four species in the York River will be discussed individually and compared with studies from other areas. Modes I and II in Figures 6 and 10 and the following discussions represent young-of-the-year (mode I) and yearlings (or older fishes, mode II), respectively, except in *M. undulatus* and Figure 16, where modes I and II represent young-of-the-year and mode III the yearlings (or older fishes).

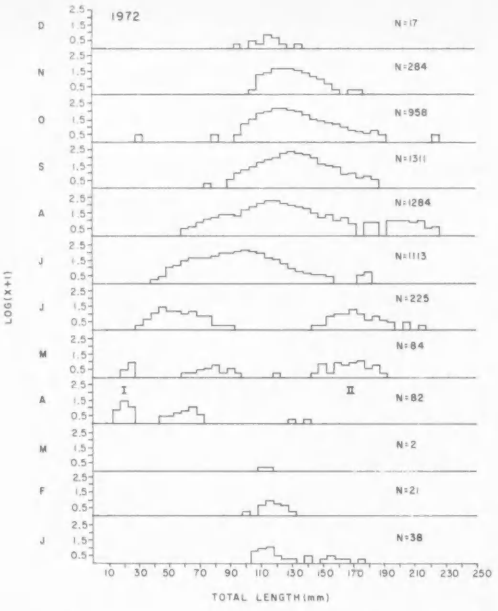
Leiostomus xanthurus Lacepède—Spot

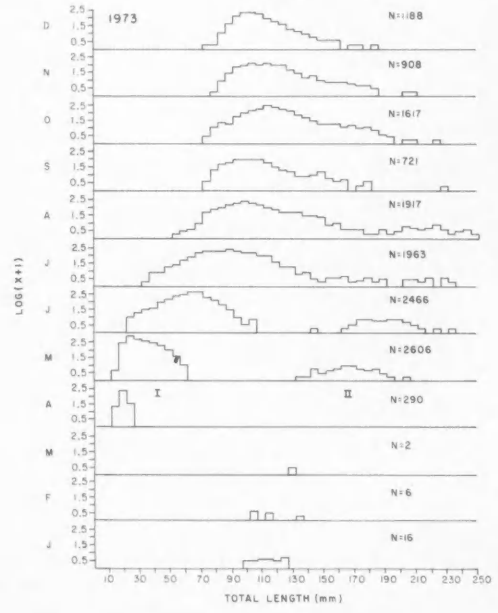
EARLY LIFE HISTORY IN THE YORK RIVER.—Young-of-the-year spot, entered the trawl and beach seine catches in early April and most left by December (Figure 6, mode I). A few smaller fish stayed in the estuary over winter. Yearling spot usually entered the study area from March to May and left the area in September (Figure 6, mode II). The intermediate mode (between modes I and II) on Figure 6, April and May 1972, was not found in the 1973 and 1974 samples. This may indicate late spawning in the previous year (1971). The length frequencies of young spot from May to July during 1972–74 were pooled and grouped by river strata (Figure 7). Young-of-the-year spot moved up to the confluence of the Pamunkey and Mattaponi rivers (Figure 1); most yearling spot stayed in the lower parts of the York River. During the same periods, no differences were found between the length frequency distributions in shoal and channel stations (Figure 8) of either young-of-the-year or yearling spot.

Spot caught in the beach seine (Figure 8) were obviously smaller than those taken by trawls. Spot was the most abundant sciaenid in the beach seine zone (depth <1.5 m) for collections with the 15.25-m and 30.5-m seines. The length frequency distribution of spot caught by beach seine was typically unimodal; mostly young-of-the-year (Figure 9). Some smaller yearlings were taken occasionally (Figure 9, 1974, mode II) and individuals >135 mm TL were captured only with the 30.5-m seine (Figure 9, August and September 1972).

In summary, young-of-the-year spot entered the York River in April and used the estuary as a nursery ground. In December, most spot left though some smaller fish stayed in the estuary through the winter, joining the yearlings as they returned to the river in the next spring. The yearlings left the estuary after an extended feeding period from March to October.

OTHER STUDIES.—Selected length frequency data for spot along the Atlantic and Gulf of Mexico coasts of the United States are summarized (Table 1) for comparison with the present study. Hildebrand and Schroeder (1928) and Pacheco (1957, 1962a) reported length frequency of spot from the present study area (York River and Chesapeake Bay). Across all areas (Table 1), young-of-the-year spot (Group 0 on Table 1) enter the estuarine nursery grounds during the first half of the year. They may enter estuaries as early as January (Table 1; Hildebrand and Cable 1930; Springer and Woodburn 1960; Sundararaj 1960). Spot first enter the





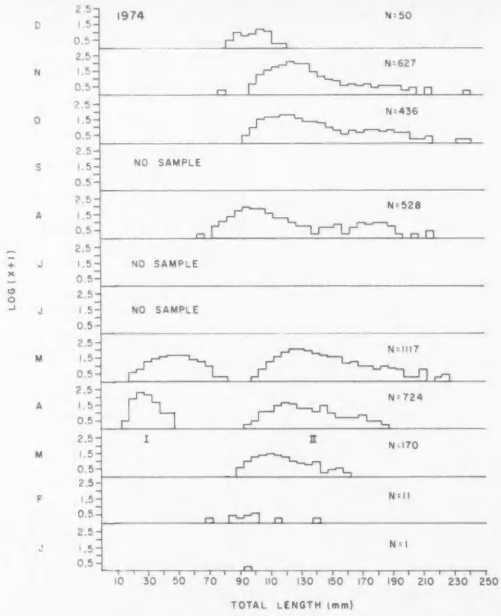


FIGURE 6.—Monthly length-frequency distributions of juvenile spot, *Leiostomus xanthurus*, from York River, 1972–74. Mode I, young-of-the-year; mode II, yearlings. Frequencies expressed as log $(x + 1)$ at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

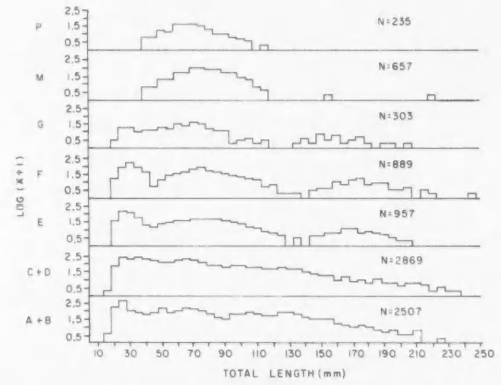


FIGURE 7.—Length-frequency distributions of spot, *Leiostomus xanthurus*, by river distance (strata) upstream in the York River estuary. Pooled total, May to July 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

estuary in February along the Atlantic coast of Georgia (Music 1974) and the Gulf of Mexico coast of Florida (Townsend 1956), Louisiana (Dunham 1972), and Texas (Parker 1971). In South Carolina (Dawson 1958; Shealy et al. 1974), North Carolina (Hildebrand and Cable 1930), and the lower Chesapeake Bay (Hildebrand and Schroeder 1928

TABLE 1.—Growth of spot, *Leiostomus xanthurus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Young 1953		Hildebrand and Schroeder 1928		Pacheco 1957		Chao 1976	
Locality	Delaware River, Del.		Chesapeake Bay, Md.		Chesapeake Bay		Lower Chesapeake Bay and York River, Va.		York River, Va.	
Period	June 1968–Sept. 1970		May–Oct. 1951		Prior to 1928		May 1955–Feb. 1956		Jan. 1972–Dec. 1974	
Gear[1]	16-ft T and S		75 x 4 ft Haul S.		?		P and 30-ft T		16-ft T and S	
Source	Table 6B		Tables 4 and 5		Table on p. 273		Table 3		Fig. 6 (present study)	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0		0	I	0	I	0	I
January						75-149		155-255		95-175
February								150-275		70-140
March					15-19					90-160
April					20-24				15-65	95-185
May			16-60		15-74	155-174	80-105	130-225	20-95	95-225
June	19.2		26-80		20-99	115-174	115-(140)	(145)-210	25-105	140-235
July	30- 80	90-140	(26-130)		40-124	135-209	115-(150)	(155)-230	35-155	155-235
August	45-100	110-165	86-90		65-149		125-(180)	(200)-245	55-(175)	(160)-250
September		120-170	86-106		94-170	190-209	135-(185)	(190)-260	70-185	230
October		125-175	(71-155)		100-184	190-299	135-(235)		80-(195)	(170)-240
November					75-184		165-(205)		80-185	(160)-240
December					75-119		155-185	220-240	75-190	

Author	Hildebrand and Cable 1930		Shealy et al. 1974		Music 1974		Townsend 1956		Springer and Woodburn 1960	
Locality	Beaufort, N.C.		South Carolina		Georgia		Alligator Harbor, Fla.		Tampa Bay, Fla.	
Period	Prior to 1930		Feb. 1973–Jan. 1974		Oct. 1970–Sept. 1973		Mar. 1955–May 1956		Jan.–Dec. 1958	
Gear[1]	PI and T		20-ft T		40-ft T, 12-ft S, 300-ft G		150- and 600-ft S		T, 80-ft S, and Pu	
Source	Tables 7 and 8		Table 27		Fig. 10		Table I		Table 13	
Length (mm)	Total length		Total length		Total length		Total length		Standard length	
Age-group[2]	0	1	0	1	0	1	0	1	0	
January	4-21	82-195		88-207		80-250			13-31	
February	3-27	91-200		83-142	10-35	85-225	10-34	95-159	13-49	
March	10-39	93-200		113-182	10-40	95-225	15-54	105-175	10-73	
April	7.5-54	84-214	18-52	107-162	15-75	95-280	20-74	105-184	19-79	
May	11-94	97-215	23-82	88-147	30-100	120-260	20-89	125-189	25-85	
June	29-119	122-198	33-(132)		40-130	135-270	60-89	145-164	31-103	
July	43-127	130-228	23-(152)		45-(170)	(170)-280	60-99	145-159	48-118	
August	67-139	140-219	48-117	153-157	45-(175)	(175)-280	75-99	165-169	49-103	
September	81-153	155-234	73-132	148-152	65-150	150-265	100-109		52-82	
October	92-170	175-269	78-127		80-150	150-250	70-124	145-169	52-97	
November	90-188	190-264	78-127		75-115	120-250	85-129		67-91	
December	1.5-9.2	84-188	83-147	168-192	65-95	100-260			76-109	

Author	Nelson 1969		Parker 1971		Pearson 1929		Sundararaj 1960		Dunham 1972	
Locality	Mobile Bay, Ala.		Galveston Bay, Tex.		Sabine River to Rio Grande, Tex.		Lake Pontchartrain, La.		Louisiana coast	
Period	May 1963-Apr. 1964		Jan. 1963–Dec. 1965		Mar. 1926–May 1927		July 1953–May 1955		July 1969–June 1972	
Gear[1]	16-ft T		4.0-m T		Tr, T, S, and G		T, Tr, S, and R		16-ft T	
Source	Table 9		Table 2		Table 31		Fig. 17		Fig. 21	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0	I	0	I	0	I	0	I
January		75-160		60-170			15-25	90-165		100-170
February		90-125	30	70-180			15-40	115-165	10-80	110-170
March		90-180	10-30	60-190			10-75	140-230	20-100	110-170
April	45-70	90-165	10-70	90-160	10-90	120-250	30-100	140-255	40-110	
May	45-(125)	(130)-171	30-100	110-190	40-120	130-250	45-120	(120)-240	50-125	
June	50-140	170-180	30-110	140-190	70-(150)	(150)-230	55-145	150-255	50-155	
July	55-145	200	30-140	170	80-140	150-230	40-160	165-250	20-155	
August	80-135		30-150	170-180	110-(220)	230-270	85-(180)	(180)-215	70-160	
September			30-160		110-(240)	250-260	95-(150)	(150)-210	90-170	110-210
October	95-(190)		50-160		110-(170)	(170)-260	90-150	170-190	120-160	
November	95-165		60-150		130-190	200-250	110-(170)	(170)-205	100-180	
December	90-175	200	70-180		130-190	200-250	135-165		70-180	

[1]Gear: G, gill net; P, pound net; Pl, plankton net; Pu, push net; R, rotenone; S, seine; T, trawl; Tr, trammel net.
[2]Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-group 0 and I is indistinguishable.

and the present study), young-of-the-year spot first entered the estuary in April (Table 1). In upper Chesapeake Bay (Young 1953) and Delaware River (Thomas 1971), young-of-the-year spot probably do not appear until May (Table 1). The smallest young-of-the-year spot from trawl catches are about 15 to 20 mm TL in all areas which indicates that the young-of-the-year spot in northern areas enter the estuary later than in southern areas. When spot first enter estuaries, gear selectivity (Table 1) affects the size ranges of spot captured; beach seines usually catch only the small specimens (Young 1953; Figure 9), but pound nets (Pacheco 1957) and large otter trawls (Music 1974) usually catch larger fishes. Offshore movements of spot during the winter season are

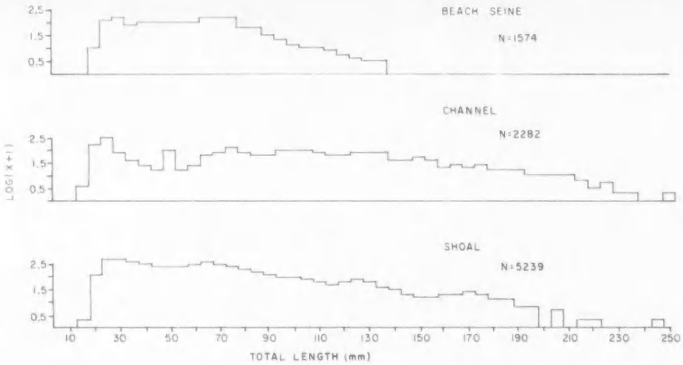


FIGURE 8.—Length-frequency distributions of spot, *Leiostomus xanthurus*, by depth of York River. Pooled total, May to July 1972–74. Frequencies expressed as log (x + 1) at 5-mm increments.

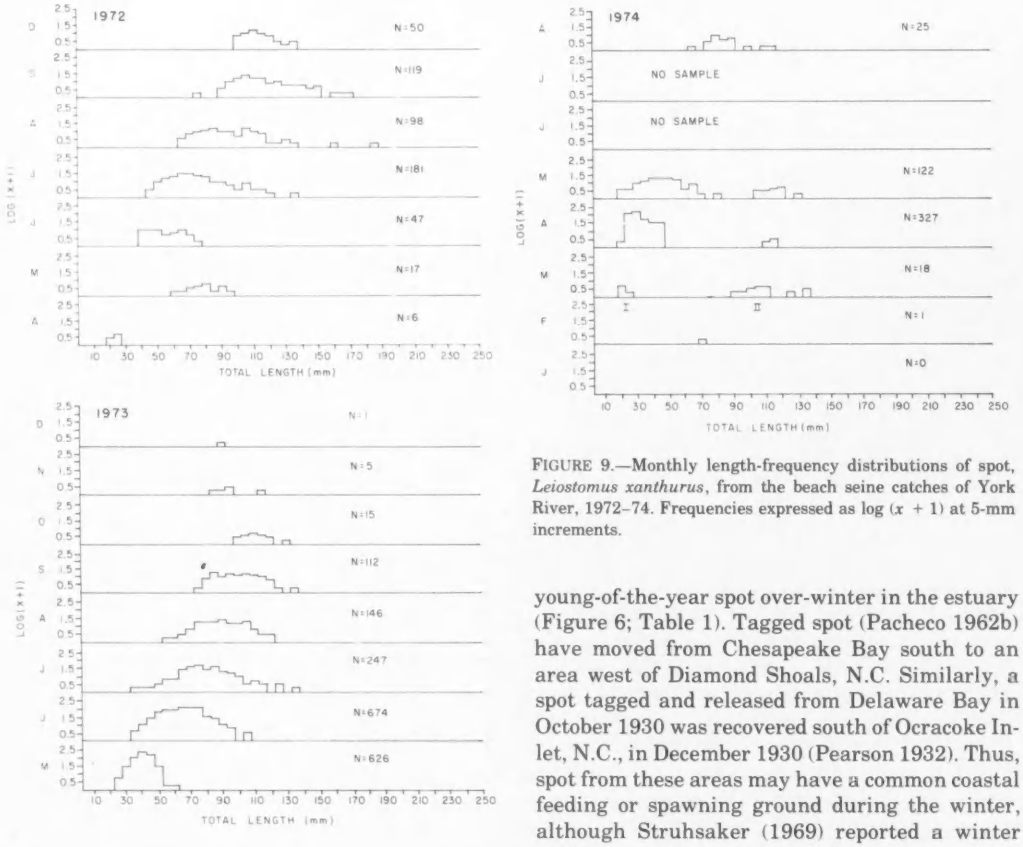


FIGURE 9.—Monthly length-frequency distributions of spot, *Leiostomus xanthurus*, from the beach seine catches of York River, 1972–74. Frequencies expressed as log (x + 1) at 5-mm increments.

evident in all areas studied because spot are completely absent or in low abundance in inshore catches. Yearling or older spot (Table 1, group I) usually leave the estuary after September and do not return until spring of the next year. Some young-of-the-year spot over-winter in the estuary (Figure 6; Table 1). Tagged spot (Pacheco 1962b) have moved from Chesapeake Bay south to an area west of Diamond Shoals, N.C. Similarly, a spot tagged and released from Delaware Bay in October 1930 was recovered south of Ocracoke Inlet, N.C., in December 1930 (Pearson 1932). Thus, spot from these areas may have a common coastal feeding or spawning ground during the winter, although Struhsaker (1969) reported a winter offshore movement of spot into deeper water (lower-shelf habitat off South Carolina). These offshore spot may be a mixture of northern and southern populations or just southern residents. The late fall or early winter spawning time of spot may be the same in both Atlantic and Gulf of

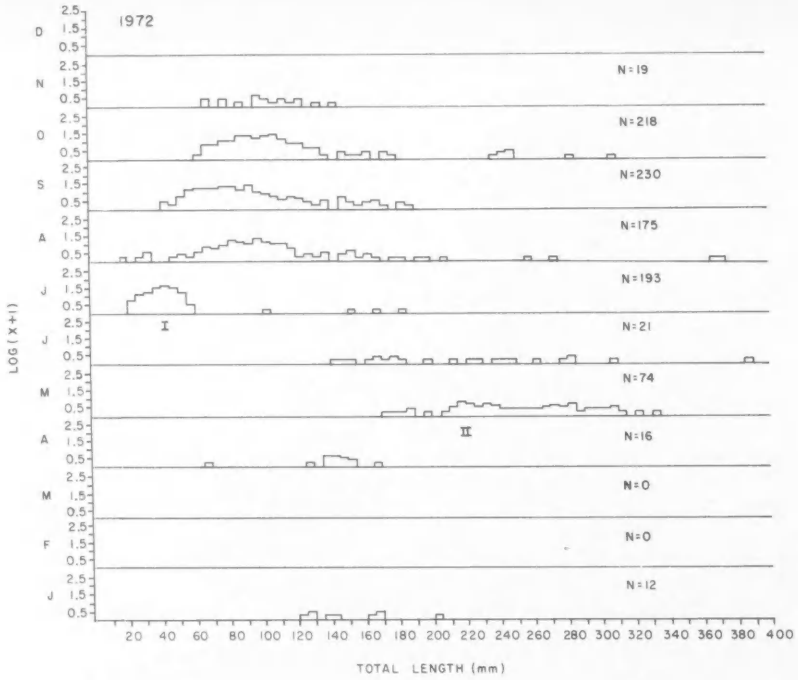
Mexico waters (Welsh and Breder 1923). Later spawning by a northern component of the population is evidenced from the length ranges of postlarvae and juvenile spot (Table 1).

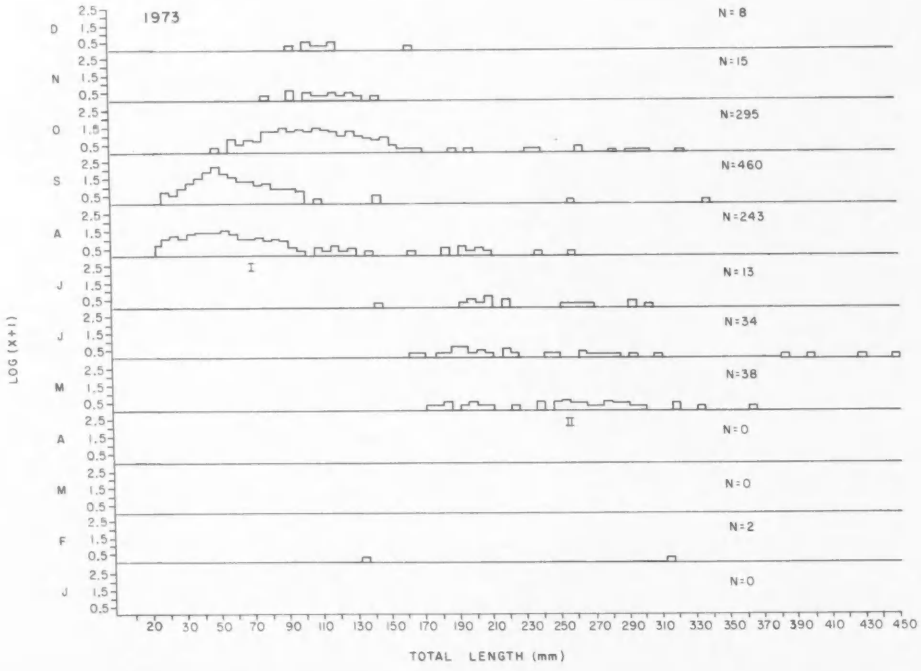
Cynoscion regalis (Bloch and Schneider)—Weakfish

EARLY LIFE HISTORY IN YORK RIVER.—Young-of-the-year weakfish first entered trawl catches in July or August and virtually left the estuary in the winter (Figure 10, mode I). Yearling weakfish returned to the river in April or May and left in September or October (Figure 10, mode II). Larger weakfish (2 yr or older) were caught only sporadically during this study because of gear avoidance. The length mode of small weakfish in August showed a rapid increase (Figure 10). This increase may be due to the recruitment of yearlings or an earlier spawned group of young-of-the-year. Length frequencies for weakfish (<250 mm TL) caught from August to October 1972–74, were pooled to compare distribution by size in the York River and its tributaries (Figure 11). Smaller fishes were more abundant in the Pamunkey and Mattaponi rivers than in the York River proper. Yearling weakfish also showed a movement upriver (Figure 11). This suggests that young weakfish entered the low salinity nursery ground (upper portion of the York River) and then moved downriver as they grew. Pooled length frequency distributions revealed an apparent difference between shoal and channel areas of the York River (Figure 12). Yearling weakfish (or larger ones) were proportionally more abundant in the channel. The 15.25-m beach seine catches contained no weakfish, but occasionally the 30.5-m seine caught some young-of-the-year weakfish in the summer.

OTHER STUDIES.—Major populations of weakfish are confined to the Atlantic coast of the United States from New York to Georgia. Existing data indicate young-of-the-year weakfish enter estuarine or coastal catches from May to July (Table 2). The smallest sizes of the weakfish in the catches differ with area and may be due to gear and/or time of sampling. Small fishes with less size variation (about 5 mm) were taken over a longer period of time in southern areas than northern areas (Table 2). Young-of-the-year weakfish do not occur in catches during winter months in northern coastal areas or estuaries (Perlmutter 1956; Massmann et al. 1958; Thomas 1971; Markle 1976). Year-round catches of weakfishes from North Carolina (Hildebrand and Cable 1934) and Georgia (Mahood 1974) were from sounds and short coastal rivers. Most of the studies suggest the age-group 0 on Table 2 was a combination of young-of-the-year and yearlings. No distinct mode could be identified for young-of-the-year from these studies. This may be due to the multiple spawning (Merriner 1973, 1976) and/or the recruitment of the young-of-the-year from different spawning populations.

The reproductive biology of weakfish is better known than other sciaenid fishes studied here. Welsh and Breder (1923) described the eggs and development of weakfish and noted that Delaware Bay was a spawning ground for weakfish. Merriner (1973) indicated that weakfish have an extended spawning season in North Carolina (March–August) and are characterized by high fecundity and possible multiple spawning by some females. Pearson (1941) took plankton tows in lower Chesapeake Bay from May to August in 1929 and 1930 and reported greater densities of weakfish larvae (1.5–17 mm TL) in subsurface tows (average 67/tow) than in surface tows (average 13/tow). The density of planktonic weakfish decreased at those stations within Chesapeake Bay, compared with sites near the bay mouth. Harmic (1958) reported that newly hatched larval weakfishes averaged 1.8 mm TL. Soon after hatching, the larvae became demersal and were dispersed into the nursery areas of Delaware Bay by means of the "salt wedge." The smallest weakfishes taken in the bottom trawl were 6 to 10 mm TL (Hildebrand and Cable 1934). The young-of-the-year weakfish in York River are probably progeny from adults spawning near the mouth of Chesapeake Bay. Weakfish tagged and released in lower Chesapeake Bay (Nesbit 1954) were later recovered to the north in New York and New Jersey, and southward in North Carolina. Nesbit (1954), Perlmutter et al. (1956), and Harmic (1958) cited the presence of a northern spawning population in New York and northern New Jersey waters and a southern spawning population from New Jersey to North Carolina. Seguin (1960) found that morphometric and meristic variation of weakfish exists along the middle Atlantic coast and suggested that three possible population segments may exist: a New York group, a Delaware and lower Chesapeake group, and a North Carolina group. Joseph (1972) questioned the


1972
D
N
O
S
A
J
J
M
A
M
F
J
N=19
N=218
N=230
N=175
N=193
N=21
N=74
N=16
N=0
N=0
N=12
I
II
LOG (X+1)
20 40 60 80 100 120 140 160 180 200 220 240 260 280 300 320 340 360 380 400
TOTAL LENGTH (mm)


1973
D
N
O
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A
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J
M
A
M
F
J
N=8
N=15
N=295
N=460
N=243
N=13
N=34
N=38
N=0
N=0
N=2
N=0
I
II
LOG (X+1)
20 30 50 70 90 110 130 150 170 190 210 230 250 270 290 310 330 350 370 390 410 430 450
TOTAL LENGTH (mm)

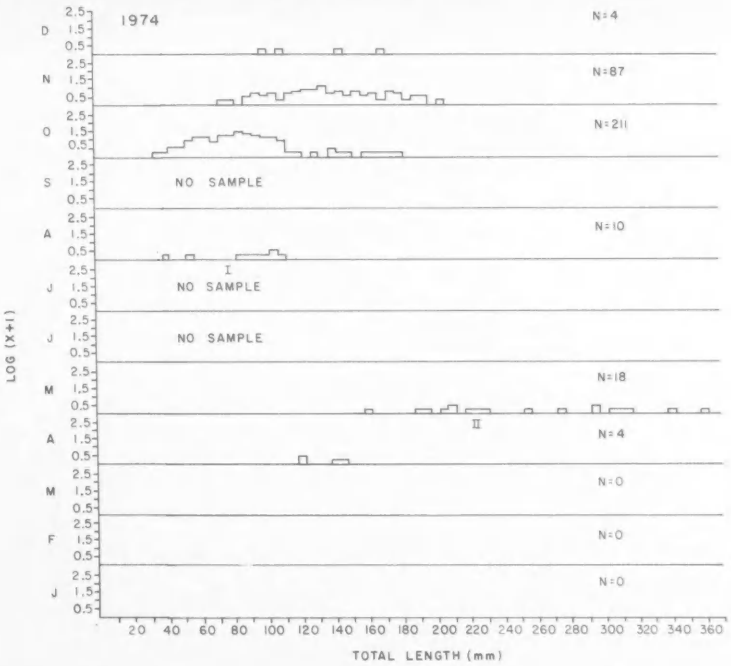

FIGURE 10.—Monthly length-frequency distributions of weakfish, *Cynoscion regalis*, from York River, 1972–74. Mode I, young-of-the-year; mode II, yearlings. Frequencies expressed as log $(x + 1)$ at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

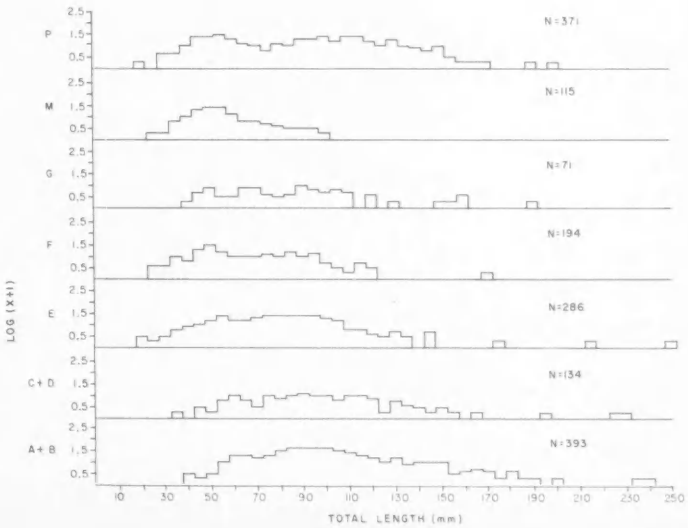

FIGURE 11.—Length-frequency distributions of weakfish, *Cynoscion regalis*, by river distance (strata) upstream of the York River estuary. Pooled total, August to October 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

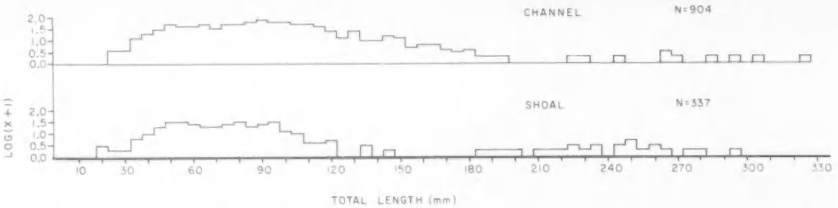

FIGURE 12.—Length-frequency distributions of weakfish, *Cynoscion regalis*, by depth of York River. Pooled total, August to October, 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

TABLE 2.—Growth of weakfish, *Cynoscion regalis*, from different estuarine areas along U.S. Atlantic coast.

Author	Thomas 1971		Pearson 1941		Chao 1976	
Locality	Delaware River, Del.		Lower Chesapeake Bay		York River, Va.	
Period	1969		1929-30		Jan. 1972-Dec. 1974	
Gear[1]	T and S		PI and P		16-ft T	
Source	Table 4		Fig. 23		Fig. 10 (present study)	
Length (mm)	Total length		Total length		Total length	
Age group[2]	0		0	I	0	I
January						120-205
February						130-315
March						
April				130-250		65-175
May						155-330
June	5-70					140-385
July	15-125		20-(150)		20-55	105-305
August	15-(185)		30-(160)		10-(95)	100-370
September	70-(185)			(130)-180	70-(110)	115-300
October	40-(175)				35-(135)	140-325
November					65-(140)	140-205
December					95-(170)	

Author	Hildebrand and Cable 1934		Shealy et al. 1974		Mahood 1974	
Locality	Beaufort, N.C.		South Carolina coast		Georgia Coast	
Period	?		Feb. 1973-Jan. 1974		Oct. 1970-Sept. 1973	
Gear[1]	PI, P, and T		20-ft T		40-ft T	
Source	Table 4		Table 32		Table 7	
Length (mm)	Total length		Total length		Total length	
Age group[2]	0	I	0	I	0	I
January		75-204		138-327		68-438
February		105-274				68-388
March		90-230		155		83-358
April		80-284		118-188		78-408
May	4-9	125-224				48-358
June	4-44	95-279	23-47	72	13-(128)	(133)-328
July	4-(39)	40-379	23-(52)	(53)-187	18-(173)	(178)-363
August	4-(64)	65-369	23-(72)	(73)-182	23-(203)	(208)-323
September	10-(79)	80-314	23-(67)	(68)-208	18-(213)	(218)-388
October	45-(94)	100-329	28-(72)	(73)-228	28-(223)	(228)-313
November	45-(99)	(100)-329	68-72	78-702	48-(233)	(238)-348
December	85-(94)	(95)-299	88-92	108-197	53-(233)	(238)-348

[1]Gear: P, pound net; PI, plankton net; S, seine; T, trawl.

[2]Age-group: 0 represents smallest groups of young-of-the-year taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable.

division of weakfish into northern and southern stocks and did not consider the decline of weakfish in Chesapeake Bay to be a result of the trawl fisheries in the shallow coastal waters and bays of North Carolina. He indicated Chesapeake Bay as a major spawning area and nursery ground, but also cited failure to obtain one weakfish larva/tow in extensive VIMS ichthyoplankton studies during 1959–63. However, weakfish eggs and larvae were reported from Chesapeake Bay by Hildebrand and Schroeder (1928) and Pearson (1941). Massmann (1963) implied that Chesapeake Bay weakfish are from southern spawning populations or stocks. Therefore, the question remains whether lower Chesapeake Bay and nearshore waters are a major spawning ground for weakfish

(Merriner 1976). Pearson (1932) described the winter trawl fishery off North Carolina and cited higher total catches of weakfish from area B (southwest of Cape Hatteras) than from area A (northeast of Cape Hatteras) in deeper waters. It is possible that most young-of-the-year and larger weakfish that leave the York River move southward to their wintering ground off Cape Hatteras. In spring, weakfish disperse from the wintering ground. Some fish move north and spawning may occur from late spring to summer along the coast from North Carolina to New York.

Bairdiella chrysoura (Lacepède)—Silver Perch

EARLY LIFE HISTORY IN THE YORK RIVER.—Silver perch were present from April to December and were most abundant from August to October (Figure 13). Total catches were reduced in 1973 and 1974. Young-of-the-year silver perch first entered the catches in July and most silver perch left the river in November. Yearlings may enter the river as early as April and most left the river in November. There were no silver perch taken from January to March during the present study (1972-74). Pooled length frequencies from August to October, 1972 to 1974, indicated that silver perch were most concentrated in the lower part of the York River (Figure 14) and larger specimens tended to stay in the channel (Figure 15). The 30.5-m beach seine caught young-of-the-year occasionally but the 15.25-m seine rarely caught any silver perch.

OTHER STUDIES.—Silver perch occur along the U.S. coast from New York to Texas. The seasonal distribution pattern is similar in all Atlantic coastal states (Table 3). Young-of-the-year silver perch were first caught in bottom trawls during June or July. Size of the smallest young-of-the-year silver perch during a given month decreases as latitude of the nursery ground increases on the Atlantic coast and west coast of Florida (Table 3). Silver perch are present almost all year round south of Chesapeake Bay (Table 3), which may be due to the higher salinity or temperature of those study areas. The embryonic development of silver perch from Beaufort, N.C., was described by Kuntz

TABLE 3.—Growth of silver perch, *Bairdiella chrysoura*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Chao 1976		Hildebrand and Cable 1930	
Locality	Delaware River, Del.		York River, Va.		Beaufort, N.C.	
Period	1969		Jan. 1972-Dec. 1974		Spring 1926-Summer 1927	
Gear[1]	16 ft T		16 ft T		Pl and T	
Source	Table 28		Fig. 13 (present study)		Tables 5 and 6	
Length (mm)	Total length		Total length		Total length	
Age-group[2]	0		0	I	0	I
January						74-204
February						90-209
March						98-204
April						93-195
May				85-200	1-6	85-204
June	5-20			145-185	1-38	110-210
July	5-65		20-60	120-190	9-76	105-224
August	45-100		15-85	100-205	20-92	130-204
September	70-120		65-135	160-210	45-122	135-189
October	65-130		60-135	160-220	73-115	145-224
November			70-155	210	68-143	150-229
December			73-110		78-124	
Author	Shealy et al. 1974		Springer and Woodburn 1960		Reid 1954	
Locality	South Carolina coast		Tampa Bay, Fla.		Cedar Key, Fla.	
Period	Feb. 1973-Jan. 1974		Oct. 1957-Dec. 1958		June 1950-May 1951	
Gear[1]	20 ft T		T, S, and Pu		15 ft T, S, and Pu	
Source	Table 42		Fig. 12		Fig. 10	
Length (mm)	Total length		Standard length		Standard length	
Age-group[2]	0	I	0	I	0	I
January	18-(72)	93-182		67		55-60
February		88-137		52-76		
March		98-172		67-73		65-95
April		73-182				
May		113-152	13-25		5-40	84-110
June		123-132	16-52		15-50	
July	33-87	128-192	16-70		20-70	
August	58-107	143-172	16-82		5-80	
September	73-132	138-177	25-85		10-82	
October	78-(187)		28-91		40-95	
November	98-(172)		19-97		50-70	
December	98-(182)		46-106			

[1]Gear: Pl, plankton net; Pu, puchnet; S, seine; T, trawl.
[2]Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable.

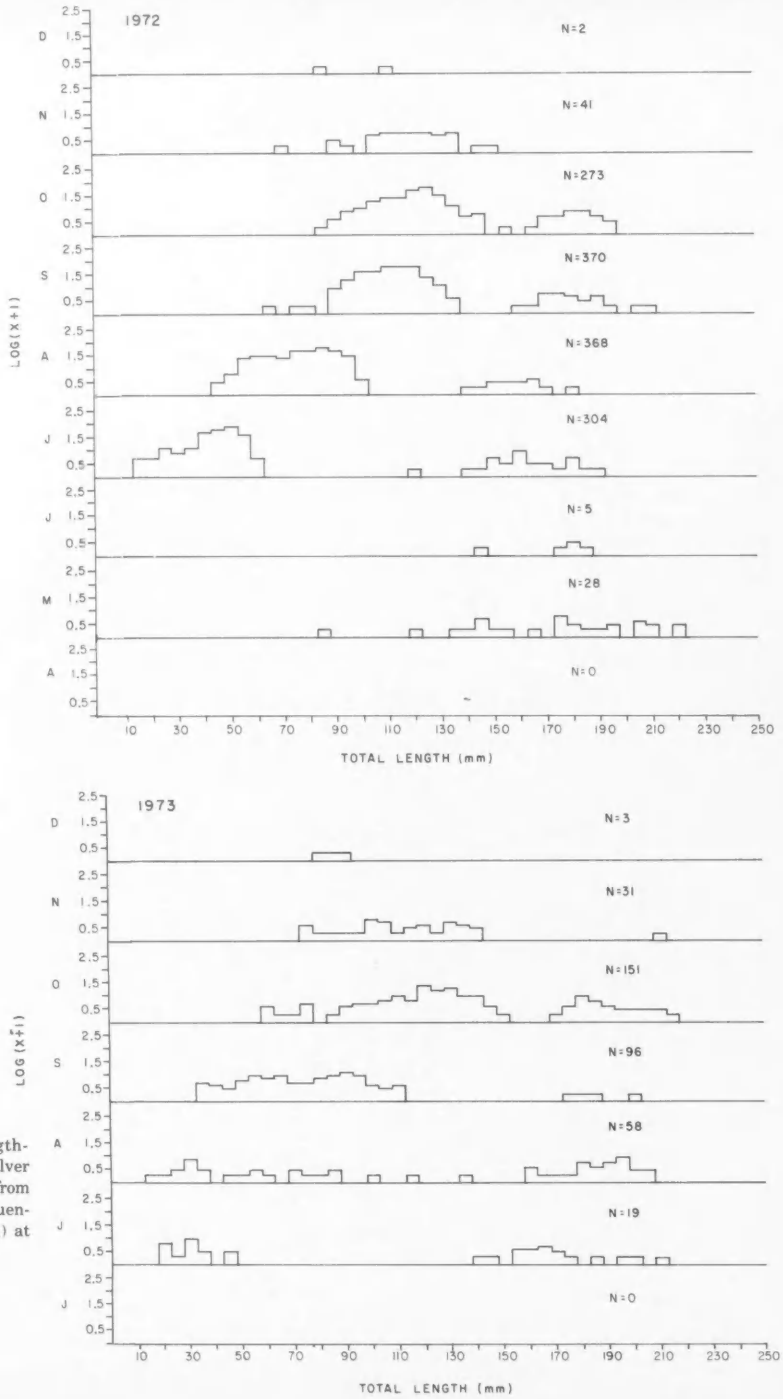

FIGURE 13.—Monthly length-frequency distributions of silver perch, *Bairdiella chrysoura*, from York River, 1972–73. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

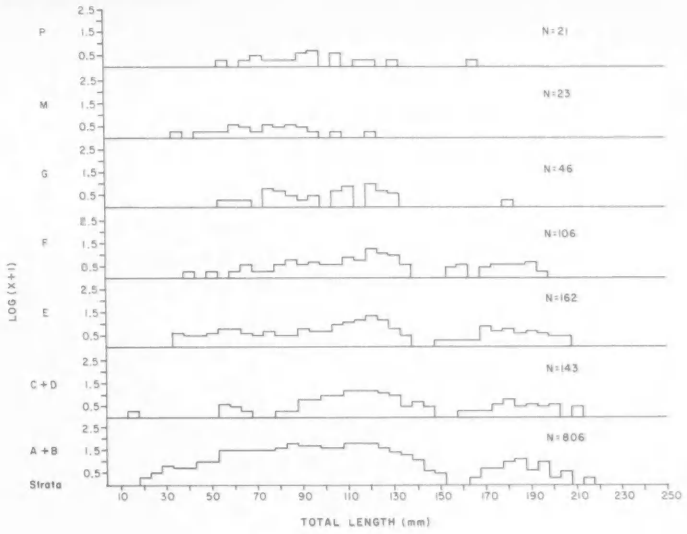

FIGURE 14.—Length-frequency distributions of silver perch, *Bairdiella chrysoura*, by river distance (strata) upstream of the York River estuary. Pooled total, August to October 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

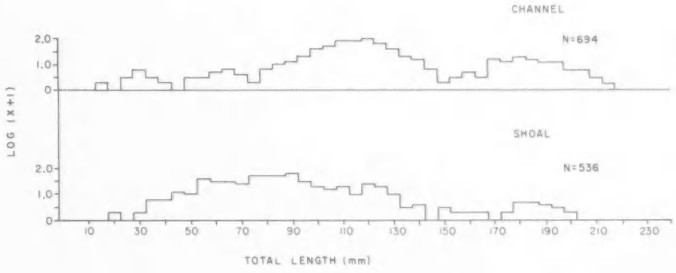

FIGURE 15.—Length-frequency distributions of silver perch, *Bairdiella chrysoura*, by depth of York River. Pooled total, August to October 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

(1914). Welsh and Breder (1923) made further observations from material obtained at Atlantic City, N.J. Jannke (1971) described larval silver perch from the Everglades National Park, Fla., and showed that larvae of 2 to 3 mm "notochord" length were present all year round. Hildebrand and Schroeder (1928) reported ripe fish of both sexes in Chesapeake Bay (24 m deep, off Chrisfield, Md.) as early as 16 May. This suggests that silver perch may spawn in the deeper waters of lower Chesapeake Bay and nearshore waters in late spring and early summer. Because of its relatively small size, commercial landings of silver perch are relatively small. Silver perch move oceanward and probably to the south of Chesapeake Bay in winter. Large numbers captured by commercial haul seines between Virginia Beach, Va., and Kitty Hawk, N.C., have been observed in fall (J. A. Musick, pers. obs.).

Micropogonias undulatus (Linnaeus)—Atlantic Croaker

EARLY LIFE HISTORY IN YORK RIVER.—Young-of-the-year croaker first entered the trawl and beach seine catches in August and stayed in the York River throughout the winter (Figure 16, mode I). They left the estuary between August and September of the following year as yearlings (Figure 16, mode III). Large croaker (more than 1.5 yr old) were caught only sporadically in this study due to gear avoidance, but they were present from February to September. There were apparently two to three length groups (modes) of young-of-the-year croaker in September 1972–74. Mode II was different from mode I and mode III of 1972 and 1974 (Figure 16). The former group did not stay in the York River over winter, but entered the estuary as early as May (Figure 16, mode II). Most of this group left in November 1972–74.

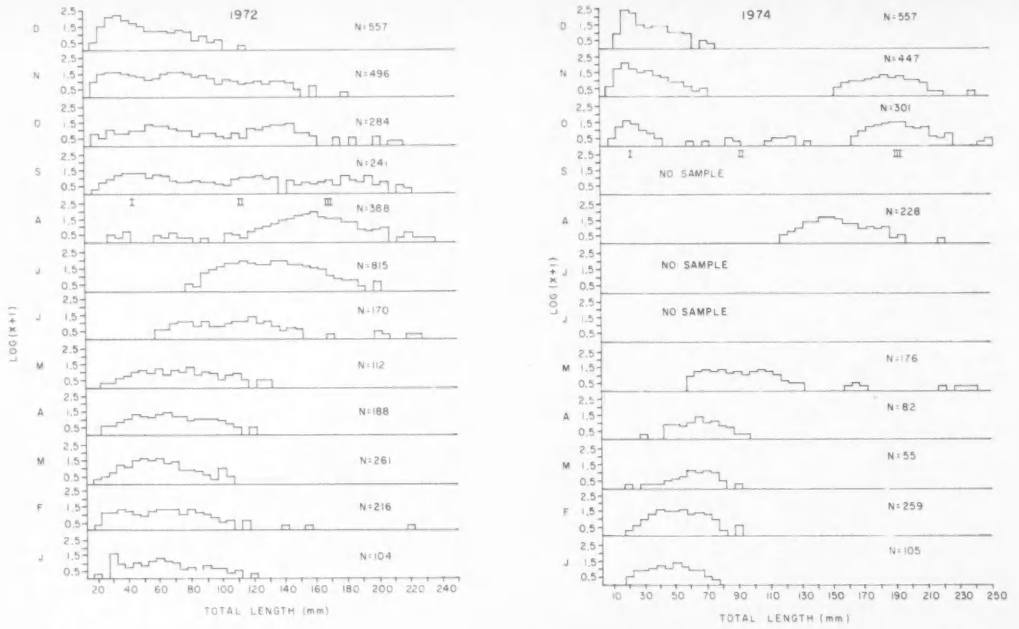

FIGURE 16.—Monthly length-frequency distributions of croaker, *Micropogonias undulatus*, from York River, 1972–74. Modes I and II, young-of-the-year; mode III, yearling. Frequencies expressed as log $(x + 1)$ at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

Size may be a determining factor for migration of young croakers from the York River. From 1972 to 1974, length frequencies (Figure 16) indicated that very few young-of-the-year croakers >130 mm TL stayed in the York River during the winter months. Young-of-the-year croakers were present in the York River in large numbers all year round except during the summer months (June–August). Young croakers showed slower growth rates over winter (Figure 16). Those entering the estuary between September and November were the main strength of the year class (modes I and III of Figure 16). Whether they represent progeny from a different spawning population compared with the earlier group (mode II of Figure 16) is unknown at present.

Length frequencies of croakers taken between September and November 1972–74 were pooled to compare distribution by size in the York River (Figure 17). The size composition indicated that smaller fish were caught in the upper part of the York River and saline portions of the Mattaponi and Pamunkey rivers. Larger fish were proportionally more abundant in the lower part of the river. Larger fish also constituted a larger portion of the croaker catch in the channel than in the shoal area (Figure 18). The 30.5-m beach seine

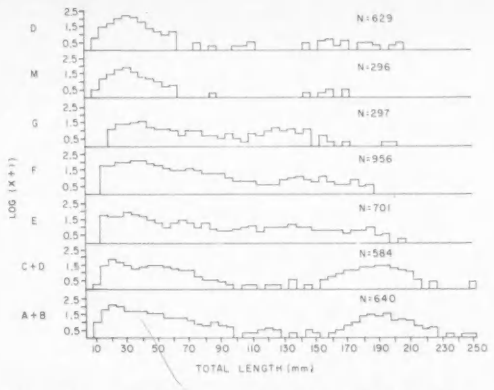

FIGURE 17.—Length-frequency distributions of croaker, *Micropogonias undulatus*, by river distance (strata) upstream of the York River estuary. Pooled total, September to November 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

(Figure 19) caught yearlings exclusively. The 15.25-m seine caught almost no croakers.

In summary, young-of-the-year croaker entered the estuary in May and from August on. The earlier group entered in May and left the estuary in November, as did older year classes. The later group (August–November) stayed in the estuary until the summer months of the following year. Young croaker moved to the upper part of the York River and the saline portions of major tributaries after first entry, then moved down the York River into more saline waters as they grew. Smaller fishes (<130 mm TL) stayed in the river throughout the winter.

OTHER STUDIES.—Croakers occur from the Gulf of Maine to Argentina, along the coasts of the Atlantic and Gulf of Mexico. Length-frequency distributions exist for different areas of the United States [see Wallace (1940) and Haven (1957) for the lower Chesapeake Bay and York River (Table 4)]. Studies usually show that small croakers (10–20 mm TL) are present in the estuary during all except the summer months (June–August). Croakers seemingly have a long spawning season since small individuals (<20 mm TL) are present from September to May in different estuarine areas (Table 4). Some croakers may be very small (<15 mm TL) in spring because of slow growth of fish spawned late in winter, or because they were spawned in spring. Such a group was also found in the present study (Figure 16, mode II) but not in previous Chesapeake Bay studies. Croakers from Maryland and Virginia tagged by Haven (1959) showed springtime movement of croakers up the estuaries and up Chesapeake Bay, and oceanward and southerly in fall (some recoveries were from off the North Carolina coast). Pearson (1932) reported a high percentage of croakers in the catches of the commercial trawl fishery during November (88%) and December (76%) from the fishing grounds off the North Carolina coast. Hildebrand and Cable (1930) implied that croaker spawning probably began in August in Chesapeake Bay and northward, in September at Beaufort (North

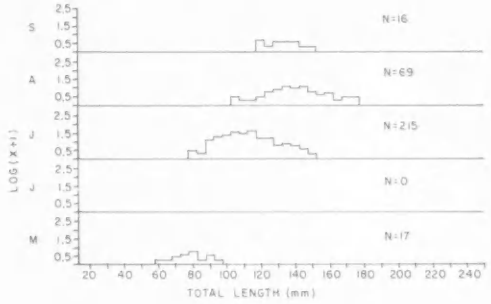

FIGURE 19.—Length-frequency distributions of croaker, *Micropogonias undulatus*, from beach seine catches of York River, May to September 1972. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

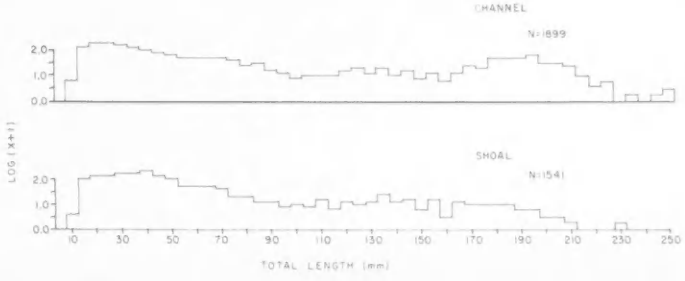

FIGURE 18.—Length-frequency distributions of croaker, *Micropogonias undulatus*, by depth of York River. Pooled total, September to November 1972–74. Frequencies expressed as log $(x + 1)$ at 5-mm increments.

TABLE 4.—Growth of croaker, *Micropogonias undulatus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Haven 1957		Chao 1976		Hildebrand and Cable 1930		Shealy et al. 1974	
Locality	Delaware River, Del.		York River, Va.		York River, Va.		Beaufort, N.C.		South Carolina coast	
Period	June 1968-Dec. 1970		Oct. 1952-July 1953		Jan. 1972-Dec. 1974		Spring 1926-Summer 1927		Feb. 1973-Jan. 1974	
Gear[1]	16-ft T		30-ft T		16-ft T and S		T and PI		20-ft T	
Source	Table 70		Fig. 7		Fig. 16 (present study)		Tables 9 & 10		Table 22	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0	I	0	I	0	I	0	I
January			15-(85)	(95)-105		20-120	3-24	25-269	18-97	108-297
February			10-60	(45)-100		20-155	3-29	40-294	28-82	113-187
March			10-(70)	(70)-120		20-175	2-24	40-294	13-102	123-173
April			10-(65)	70-100		25-120	25-19	100-259	18-(132)	138-192
May			25-(90)	70-140	20-30	(20)-240	8-25	195-239	28-112	
June			40-(120)	(120)-155	20-70	(60)-245		31-284	33-142	
July			75-145	(135)-175	30-(110)	(80)-250		43-234	28-(182)	
August			N.S.	N.S.	30-(90)	(70)-240		66-289	53-177	
September			N.S.	N.S.	10-(100)	(70)-195	2-9	80-279	78-182	
October	20	135-140	10-(40)	(40)-85	10-(110)	(100)-250	2-50	98-294	68-182	
November	25		15-(60)	(60)-115	15-100	(60)-250	1.5-66	85-284	43-153	
December	20-50		10-(60)	(60)-120	20-110	165-175	2.5-69	85-259	48-163	183-197

Author	Hoese 1973		Hansen 1969		Suttkus 1955		Parker 1971	
Locality	Georgia coast		Pensacola, Fla.		Lake Pontchartrain and Louisiana coast		Galveston Bay, Tex.	
Period	Aug. 1956-Aug. 1966		Aug. 1963-Dec. 1965		July 1953-Oct. 1954		Jan. 1963-Dec. 1965	
Gear[1]	30- and 40-ft T		5-m T		T and S		4.9-m T	
Source	Fig. 12		Fig. 2		Table 1		Fig. 21	
Length (mm)	Total length		Total length		Total length		Total length	
Age-group[2]	0	I	0	I	0	I	0	I
January	10-80	120-130	15-20	45-95	10-79	120-189	10-(80)	90-200
February	20-80		20-25	40-95	10-89	130-179	10-(90)	(90)-250
March	20-80	110-120	15-35	75-85	20-119	120-259	10-(90)	(100)-250
April	40-100		N.S.	N.S.	20-129	130-339	10-(120)	(130)-250
May	20-110		20-(75)	(60)-135	30-139	140-319	10-(130)	(130)-240
June	50-140	200-210	30-(95)	(90)-150	30-139	140-329	40-(140)	(156)-250
July	60-140		35-(90)	(90)-145	50-159	160-380	30-(150)	(160)-230
August	90-160	190-200	35-(110)	(100)-150	80-169	170-319	60-160	170-250
September	60-150		40-(90)	(90)-150	80-169	170-319	60-(170)	(170)-190
October	100-180		45-(110)	(110)-150	90-189	(170)-349	10-40	60-220
November			50-105		20-59	130-309	10-(60)	60-210
December			10-95		10-79	120-299	10-(70)	70-230

[1]Gear: PI, plankton net; S. seine; T. trawl.
[2]Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable. N.S.; no sample.

Carolina), and in October in Texas. Arnoldi et al. (1973) "tagged" young-of-the-year croakers (9-48 mm TL). Their successful recaptures indicated that individual croaker remained in the particular marsh for only 1 to 4 mo, which was much shorter than the total length of time croaker were observed in the marsh (October–June). Thus, they also suggested that several croaker "populations" may utilize coastal marsh as nursery ground during the course of the year. White and Chittenden (1977) indicated that some croakers in the Gulf of Mexico may lack the first (overwinter) ring on the scales. This suggests that some croakers may spawn in the spring in the Gulf of Mexico.

Massmann and Pacheco (1960) reported the disappearance of young croakers from the York River, but their conclusion may have been in error because of selectivity of their fishing gear. Haven's (1957) length frequencies for croakers during 1952 and 1953 differ from those presented by Massmann and Pacheco (1960) for the same years. No fish <100 mm TL were reported by Massmann and Pacheco (1960), but their gear was a net with ¾-in (about 1.9-cm) mesh, whereas Haven (1957) used ¼-in (about 0.6-cm) mesh. Joseph (1972) attributed the decline of croaker in the commercial catches of the middle Atlantic coast to climatic trends. Present data support his hypothesis. The apparent increase in juvenile croakers in 1973 and 1974 was probably due to warmer winter months. Mean bottom temperatures of the York River channel were about 3.6°C and 3.2°C in January and February, respectively, from 1967 to 1971 (Markle 1976). It was 6.7°C for January and 6.3°C for February in 1973 and 1974 (Figure 2). The year class strength of croaker in the York River was dependent on the success of the late young-of-the-year group (Figure 16, mode I), which stayed in the estuary through the winter. Historical York River trawl data show mass mortalities of young-of-the-year croaker during some cold winters (VIMS, Ichthyology Department, unpubl. data).

Feeding Mechanisms

The Sciaenidae have the widest spectrum of

feeding niches of any fish family in the Chesapeake Bay. The four most abundant species, *Cynoscion regalis, Bairdiella chrysoura, Micropogonias undulatus,* and *Leiostomus xanthurus,* are most abundant in the estuary from late spring to fall, especially young-of-the-year and yearlings (see previous sections). Under these conditions, food resources may be limiting and division of feeding niches may have evolved in order to reduce competitive exclusion among the dominant species. Fishes that are closely related and show feeding niche segregation also often show morphological differentiation in the feeding apparatus (Keast and Webb 1966; Davis 1967; Keast 1970; Davis and Birdsong 1973; Emery 1973). This section of the paper examines the morphology of the feeding apparatus in *Larimus fasciatus, C. regalis, B. chrysoura, M. undulatus, Menticirrhus saxatilis,* and *Leiostomus xanthurus* to test the hypothesis that adaptations to feeding niche division have evolved among those six species.

Characters important in feeding were examined including mouth position and size, dentition, number of gill rakers, and intestine length. These directly affect the size and kind of food ingested and digested. Other accessory characters examined were the pore and barbel system on the snout and/or lower jaw, the nares, and body shape.

Mouth Position

Mouth position and size of the opening limit the size of prey and habitats in which a predator can effectively capture prey. These characters were

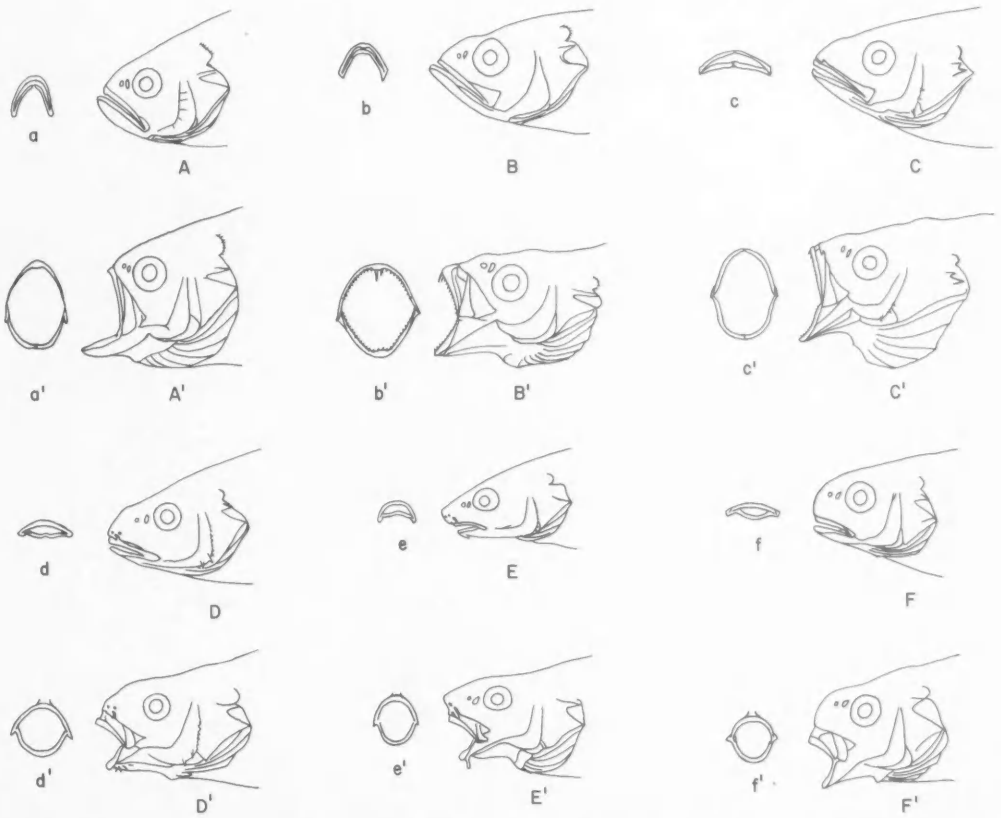

FIGURE 20.—Mouth position and opening in juveniles of six species of sciaenids: A, A′, a, a′, *Larimus fasciatus;* B, B′, b, b′, *Cynoscion regalis;* C, C′, c, c′, *Bairdiella chrysoura;* D, D′, d, d′, *Micropogonias undulatus;* E, E′, e, e′. *Menticirrhus saxatilis;* F, F′, f, f′, *Leiostomus xanthurus.* A–F, mouth closed. A′–F′ mouth wide open. Front view of mouth openings (lower case letters) in corresponding positions.

studied from freshly caught and preserved specimens. *Larimus fasciatus* has the most oblique mouth (Figure 20A) with the lower jaw projecting strongly in front of the nonprotrusible upper jaw. The maxilla (Figure 21A) is under the lateral margin of the rostral fold and its anterior end is firmly attached to the premaxilla and skull (dermethmoid). As the mouth opens, the distal ends of the premaxilla and maxillae push forward as the lower jaw is lowered (Figure 20A′). The mouth opens widely. *Cynoscion regalis* has a large oblique mouth with the tip of the lower jaw projecting in front of the nonprotusible upper jaw (Figure 20B). The anterior end of the maxilla is firmly attached to the premaxilla and articulates with the dermethmoid (Figure 21B). As the mouth is opened, the posterior end of the premaxilla and the lower jaw move forward (Figure 20B′). The mouth opens widely. *Bairdiella chrysoura* has a similar mechanism of jaw movement (Figure 20C′), but the mouth is only slightly oblique with the lower jaw about equal in length to the upper jaw (Figures 20C, 21C). *Micropogonias undulatus* has an inferior mouth with the tip of the lower jaw enclosed by the protrusible upper jaw (Figure 20D). The anterior end of the maxilla is loosely attached to the premaxilla (Figure 21D). As the mouth is opened, the entire premaxilla and the lower jaw move anteroventrally (Figure 20D′). The mouth opens widely. *Menticirrhus saxatilis* and *Leiostomus xanthurus* have a similar mechanism of jaw movement but their upper jaws seem more protrusible (Figures 20E′, F′; 21E, F). Their gape is small. In *M. saxatilis*, the mouth is inferior and the lower jaw is enclosed by the upper jaw (Figure 20E). *Leiostomus xanthurus* also has a small inferior mouth (Figure 20F) with a small gape.

The mouth position indicates that *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* are pelagic feeders (Figure 20A–C) and that *Micropogonias*

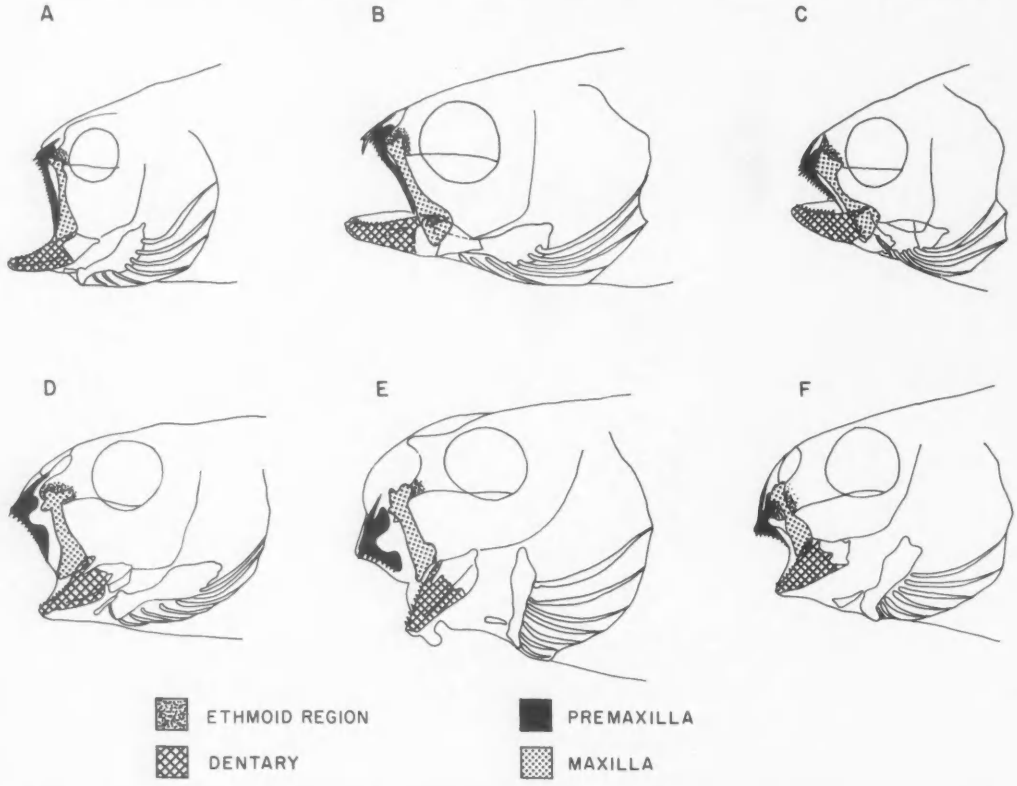

FIGURE 21.—Jaw bones involved in mouth opening in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

undulatus, *Menticirrhus saxatilis*, and *Leiostomus xanthurus* feed on the bottom (Figure 20D–F). The relative length of the premaxilla and dentary bones decreases and the height of the anterior dorsal process of the premaxilla increases from fishes adapted to feed in "midwater" to those adapted to feed on the bottom (Figure 21). This trend is also evident in the relative mouth size and angle (Figure 21A–F). An index number (Table 5), the length of the upper jaw multiplied by the length of the lower jaw then divided by head length, decreases through the series of species towards a bottom feeding habit.

Bottom feeders, *M. undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*, have protrusible premaxillae (Figures 20D′–F′, 21D–F). This can be advantageous in getting the mouth opening close to food that is to be sucked in from the bottom (Alexander 1967). Midwater feeders, *Larimus fasciatus*, *C. regalis*, and *B. chrysoura*, lack the protrusibility of the premaxillae (Figures 20A′–C′; 21A–C); *C. regalis* and *B. chrysoura* may compensate for this with faster swimming speed. Gero (1952) and Nyberg (1971) have discussed this aspect in detail. *Larimus fasciatus* differs from other sciaenids studied here. It may swim around with its mouth open using its gill rakers as a filter similar to that of *Engraulis* (Günther 1962).

Dentition

Teeth on the premaxilla and dentary are important in capturing prey whereas the pharyngeal teeth are used for grinding and/or transporting food to the esophagus. Members of the genus *Cynoscion* usually have a pair of enlarged canine teeth at the tip of the upper jaw (Figures 21B, 22B). Other teeth are conical and present on narrow bands of the premaxilla and dentary. The tips of the upper and lower jaws are broad and have several rows of teeth which decrease in number to a single prominent row on the narrower posterior portion of the jaws. Small teeth also develop inside the larger row of upper jaw teeth and outside the lower jaw teeth. *Bairdiella chrysoura* has a narrow band of teeth similar to *C. regalis* but lacks large canine teeth at the tip of the upper jaw (Figure 22C). *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* have villiform teeth set in broad bands on the premaxillae and dentaries, and also lack canine teeth (Figure 22D–F). The teeth on the outer row of the premaxillae and inner row of the dentaries are slightly enlarged. *Larimus fasciatus* is unique in having only one or two rows of small teeth on both jaws (Figure 22A).

Pharyngeal teeth are generally conical in sciaenids (Figure 23). The lower pharyngeal teeth form a pair of separate narrow tooth patches and are situated on the most medial pairs of ceratobranchial bones. The upper pharyngeal teeth occur mainly as two pairs of patches on the two most medial pairs of epibranchial bones. The pharyngeal plates are relatively small and narrow in *L. fasciatus* and *C. regalis* compared with the other sciaenids examined (Figure 23A, B). The pharyngeal teeth of *L. fasciatus* and *C. regalis* are sharp, conical, and directed backward, but in *B. chrysoura* the pharyngeal teeth are blunt and the median ones are enlarged (Figure 23C). *Micropogonias undulatus* has much stronger and more enlarged pharyngeal teeth along the median rows (Figure 23D). *Menticirrhus saxatilis* has fine and sharp pharyngeal teeth (Figure 23E). *Leiostomus xanthurus* develops molariform teeth medially on the pharyngeal plates (Figure 23F). These sequential morphological differences in pharyngeal teeth reflect the feeding niche differentiation from midwater to benthic.

Gill Rakers

Gill rakers on the branchial arches of fishes are important in protecting the delicate gill filaments

TABLE 5.—Relative size of mouth and eye diameter in juveniles of six species of sciaenids from the York River.

Species	SL (mm)	Head length (mm)	Index of mouth size[1]				Eye diameter in % of SL			
			Range	$\bar{x}$	SD	N	Range	$\bar{x}$	SD	N
Larimus fasciatus	55.3-107	18.7-36.3	3.17-5.90	4.634	0.957	20	7.38- 9.84	8.602	0.672	21
Cynoscion regalis	35.2- 75.3	12.7-29.6	1.93-3.54	2.827	0.518	22	8.20-11.45	9.55	0.782	26
Bairdiella chrysoura	38.4- 77.5	14.3-27.4	1.76-3.08	2.494	0.431	17	8.27-10.82	9.407	0.677	20
Micropogonias undulatus	35.5-116	12.1-39.3	1.20-2.41	1.686	0.325	30	6.45- 9.46	7.850	0.837	30
Menticirrhus saxatilis	29.2- 99.6	9.3-29.0	0.50-1.37	0.957	0.264	30	6.03- 8.56	7.043	0.644	30
Leiostomus xanthurus	47.4-146	18.0-41.3	0.77-2.64	1.472	0.477	30	7.05-11.11	9.139	0.889	46

[1]Index of mouth size = (upper jaw length × lower jaw length)/head length.

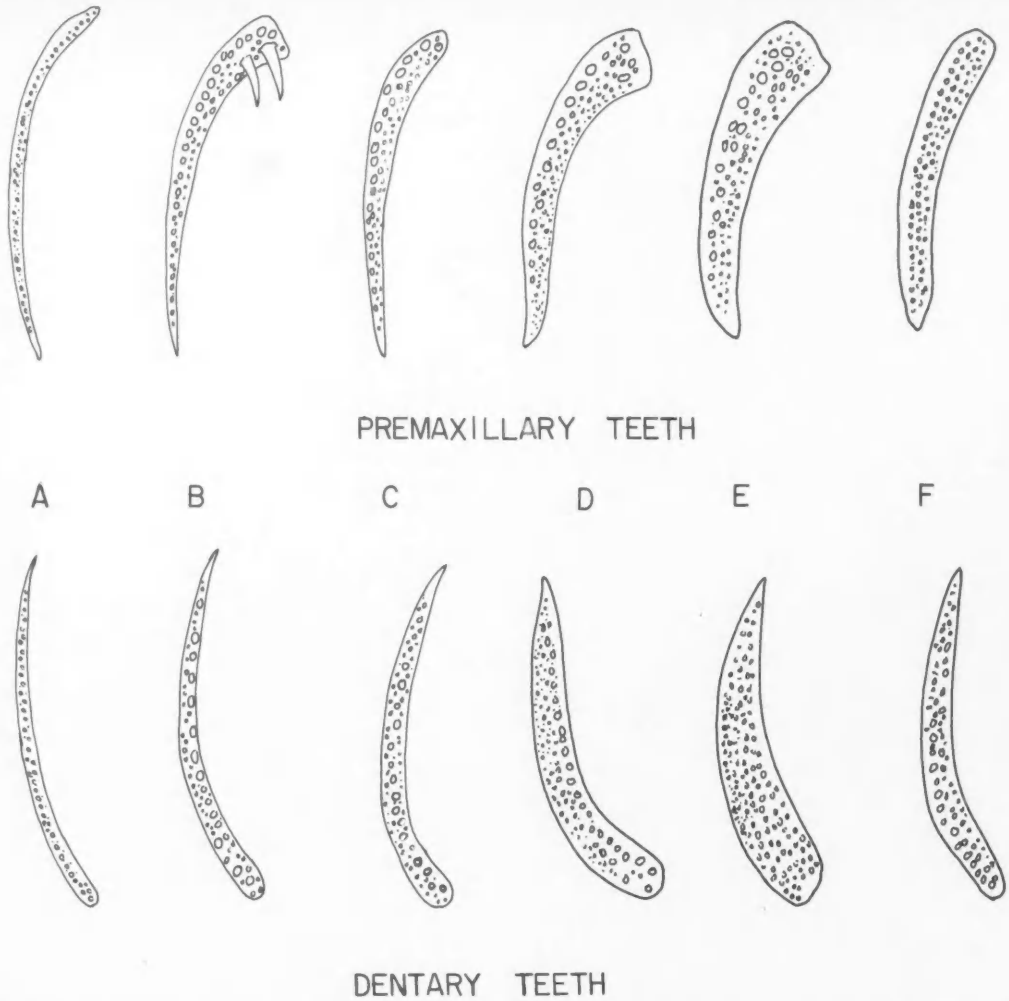

FIGURE 22.—Dentition of right premaxilla and dentary in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura* D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Posterior end toward the middle of the figure.

from abrasion by ingested materials and may also be adapted to particular food and feeding habits. In sciaenids, the gill rakers reflect feeding niche by their numbers, size, and shape. They are found on the dorsolateral surface of the branchial arch (Figure 24) and along its inner surface. The lateral gill rakers are well developed only on the first gill arch and the inner (or medial) gill rakers occur only as tubercles on all five gill arches. Only the rakers on the first gill arch are discussed here.

Menticirrhus saxatilis and *C. regalis* have the fewest gill rakers (Table 6). *Bairdiella chrysoura* and *Micropogonias undulatus* have an intermediate number and *L. xanthurus* and *Larimus fasciatus* have the most gill rakers. Numbers of inner gill rakers (Table 6) follow a similar sequence. The relative size of the gill rakers and their morphology differ among species (Figure 24).

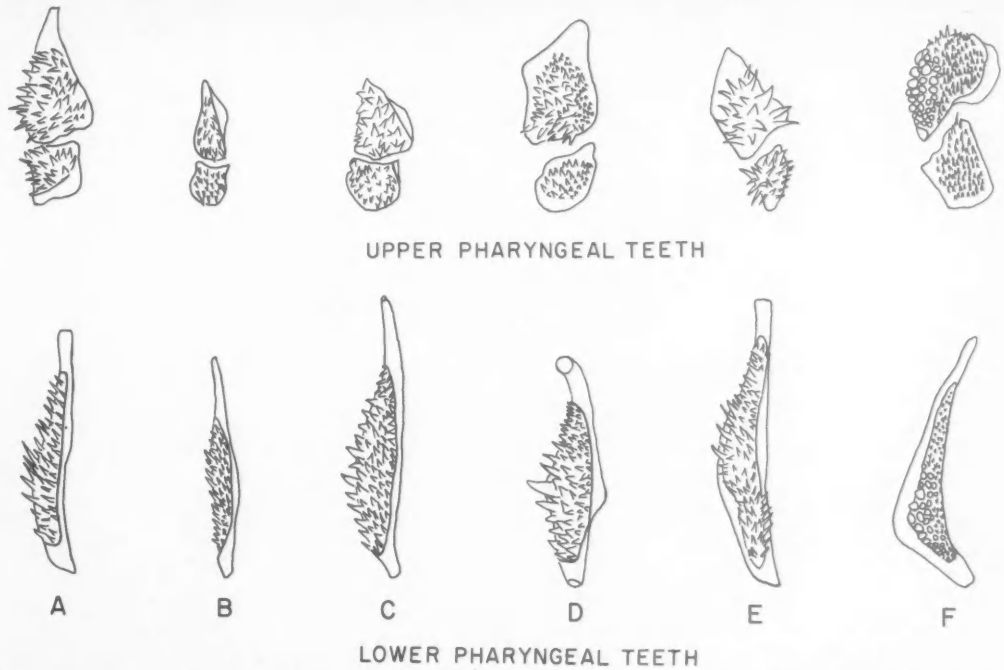

FIGURE 23.—Portions of left pharyngeal teeth in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Posterior end toward the middle of the figure.

TABLE 6.—Total number of lateral and inner gill rakers in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25			N	$\bar{x}$
Menticirrhus saxatilis						6	11	9	3	1													30	12.04
(29.2-99.6)	[5	20	4	—	1][1]																		[30]	[6.73]
Cynoscion regalis										1	8	13	13	2									37	17.19
(35.2-75.3)			[	—	4	10	8	2	2]														[27]	[11.40]
Micropogonias undulatus														1	—	3	16	15	7				42	22.55
(35.5-116)									[2	8	16	4]								1			[30]	[15.73]
Bairdiella chrysoura																2	3	13	14				33	24.27
(38.4-75.3)								[1	2	5	6	6]											[20]	[15.70]

Species (size in mm SL)	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	N	$\bar{x}$
Leiostomus xanthurus												4	7	6	12	9	13	3	1				55	32.29
(47.4-148)						[1	1	4	9	7	14	6	2]										[44]	[27.18]
Larimus fasciatus																		5	9	5	2	1	22	38.00
(55.3-107)	[1	1	5	7	4	2	1]																[21]	[21.04]

[1] [ ] medial gill rakers.

Larimus fasciatus has the longest and the most closely spaced gill rakers (Figure 24A). Each raker has many minute spicules scattered on it (Figure 24a). *Cynoscion regalis* and *B. chrysoura* have moderately long gill rakers compared with the length of the gill filaments (Figure 24B, C). Numerous minute spicules are also present on each raker, especially the basal portion (Figure 24b, c). *Micropogonias undulatus* has relatively shorter gill rakers (Figure 24D) with seemingly strong serrations limited to the basal half of the raker (Figure 24d). The relative lengths of the lateral gill rakers in *Menticirrhus saxatilis* and *Leiostomus xanthurus* are the shortest (Figure 24E, F) and lack strong spicules (Figure 24e, f). *Leiostomus xanthurus* has only slightly denticulate gill rakers and *M. saxatilis* has smooth gill rakers.

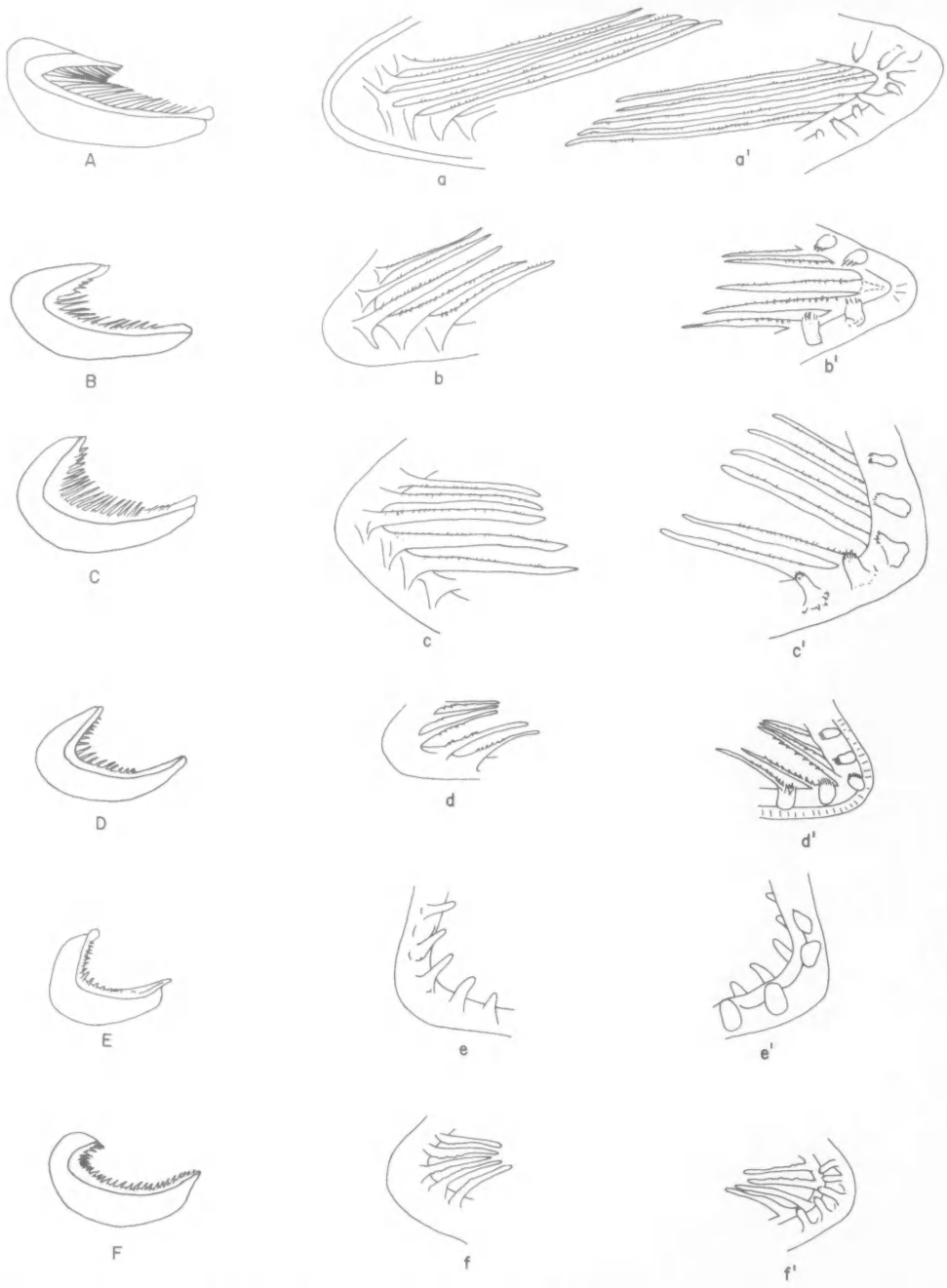

FIGURE 24.—First right gill arch in juveniles of six species of sciaenids: A, a, a′, *Larimus fasciatus*; B, b, b′, *Cynoscion regalis*; C, c, c′, *Bairdiella chrysoura*; D, d, d′, *Micropogonias undulatus*; E, e, e′, *Menticirrhus saxatilis*; F, f, f′, *Leiostomus xanthurus*. a–f, lateral view at the corner, a′–f′, medial view at the corner.

The inner gill rakers are knoblike, sometimes with spicules or teeth on their distal ends (Figure 24a′–f′). *Cynoscion regalis*, *Micropogonias undulatus*, and *Menticirrhus saxatilis* have broad, short inner gill rakers, with the height not longer than the width of the base. *Cynoscion regalis* and *Micropogonias undulatus* have prominent spicules at the distal ends of their inner gill rakers (Figure 24b′, d′). *Menticirrhus saxatilis* lacks spicules on its inner gill rakers (Figure 24e′). *Larimus fasciatus*, *B. chrysoura*, and *Leiostomus xanthurus* have long inner gill rakers, with the height longer than the width of the base. *Larimus fasciatus* and *B. chrysoura* have prominent spicules at the distal ends of their inner gill rakers (Figure 24b′, c′). *Leiostomus xanthurus* has minute spicules on its inner gill rakers (Figure 24f′). Furthermore, in *Larimus fasciatus* a small inner gill raker is often present in between the larger inner gill rakers (Figure 24a′). This is rather common among western Atlantic sciaenids (Chao in press).

The lateral and inner gill rakers on the second to fifth gill arches are similar in size and structure to the inner gill rakers on the first gill arch. The gill arches of these six species also differ in the relative lengths of the epibranchial (upper) arm and ceratobranchial (lower) arm (Figure 24). *Leiostomus xanthurus* has the shortest upper arm and *M. saxatilis* has the shortest lower arm. The numbers and size of the gill rakers indicate that midwater feeders have lateral rakers longer than those of bottom feeders. The relative lengths of inner rakers are longer in fishes with higher numbers of lateral rakers, e.g., *Larimus fasciatus* and *Leiostomus xanthurus* (Figure 24a′, f′; Table 6). Although *Micropogonias undulatus* has the strongest spicules on the lateral gill rakers (Figure 24d), the midwater feeders usually have better developed spicules on the lateral rakers than the bottom feeders (Figure 24). Higher numbers of rakers (both inner and lateral) are associated with filter feeding.

Digestive Tract

The digestive tract of sciaenids includes four parts: esophagus, stomach, pyloric caeca, and intestine. The intestine usually has two loops (Figure 25), except that of *C. regalis* which is a straight tube from stomach to anus (Figure 25B). The relative position and size of the stomach and intestine vary with the amount of food present. The numbers of pyloric caeca and the relative length of the intestine may be correlated with feeding habits (Suyehiro 1942). The relative length of the intestine of these six species of sciaenid fishes (Table 7) may be grouped into three general categories. *Cynoscion regalis* has the shortest intestine, less than half the standard length. *Bairdiella chrysoura* has an intermediate intestine length. *Micropogonias undulatus*, *Menticirrhus saxatilis*, *Larimus fasciatus*, and *Leiostomus xanthurus* have long intestines. The numbers of pyloric caeca (Table 8) in these six sciaenid fishes show a similar trend. *Cynoscion regalis* has the fewest pyloric caeca, four or five. *Bairdiella chrysoura* and *M. saxatilis* usually have 6 or 7, and *Micropogonias undulatus* and *L. xanthurus* have 7 to 10 pyloric caeca. *Larimus fasciatus* has the most, 10 or 11. *Larimus fasciatus* and *Leiostomus xanthurus* have both a longer intestine and more pyloric caeca, but *Larimus fasciatus* is a midwater feeder and *Leiostomus xanthurus* is a bottom feeder. They both consume large numbers of small crustaceans (see "Food Specialization" section). *Cynoscion regalis* has the shortest intestine and the fewest pyloric caeca. Its diet is mainly composed of large crustaceans and fishes. Thus, the relative lengths of the intestine and the numbers of pyloric caeca in these sciaenids may be correlated with the size of the food rather than the feeding position in the water column.

TABLE 7.—Relative length of intestine in juveniles of six species of sciaenids from the York River.

Species	SL (mm)	Intestine length in % of SL			
		Range	$\bar{x}$	SD	*N*
Cynoscion regalis	35.2-152	35.5-49.6	40.24	3.07	36
Bairdiella chrysoura	30.0-151	46.1-64.1	55.34	5.92	30
Micropogonias undulatus	35.5-145	52.3-88.6	65.57	6.56	39
Menticirrhus saxatilis	29.2-91.2	56.6-88.2	76.06	6.67	26
Larimus fasciatus	35.3-99.8	73.1-97.7	83.87	9.08	14
Leiostomus xanthurus	47.4-166	73.6-97.8	84.69	6.95	30

TABLE 8.—Number of pyloric caeca in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	4	5	6	7	8	9	10	11	*N*	$\bar{x}$
Cynoscion regalis (35.2-82.4)	20	14							34	4.41
Bairdiella chrysoura (30.0-75.3)			8	20	1				29	6.76
Menticirrhus saxatilis (29.2-99.6)			11	19					30	6.63
Micropogonias undulatus (35.5-116)				1	25	11			37	8.27
Leiostomus xanthurus (47.4-148)				6	13	8	1		28	8.14
Larimus fasciatus (55.3-107)							9	6	15	10.4

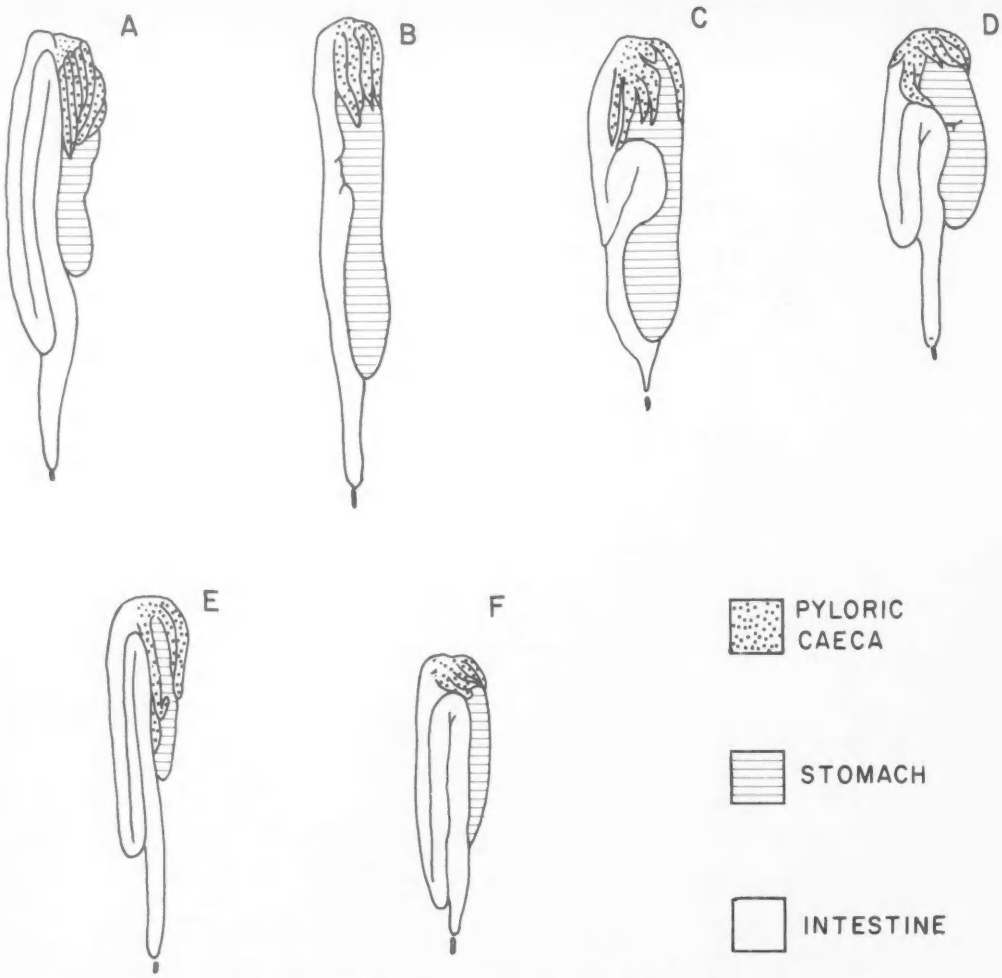

FIGURE 25.—Ventral view of the digestive tract in juveniles of six species of scaienids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

Pores and Barbels

The pores on the snout and the tip of the lower jaw, and mental barbels in fishes are sense organs probably involved in touch, taste, or both. The number and arrangement of the pores and barbels in sciaenid fishes are closely related to their feeding habitats (Chao 1976). These six species of sciaenid fishes show a gradual increase in the number and size of pores from upper water column feeders to lower water column and bottom feeders (Figure 26). *Larimus fasciatus* has five marginal pores on the snout and four minute pores at the tip of the underside of the lower jaw (Figure 26A, a). *Cynoscion regalis* has only two marginal pores on the snout and no pores or barbels on the lower jaw (Figure 26B, b). *Bairdiella chrysoura* has five marginal and five upper pores on the snout, and six mental pores at the tip of the lower jaw (Figure 26C, c). *Leiostomus xanthurus* has five marginal and five upper pores on the snout, and five mental pores at the tip of the lower jaw (Figure 26F, f).

Micropogonias undulatus also has five marginal and five upper pores on the snout, and five mental

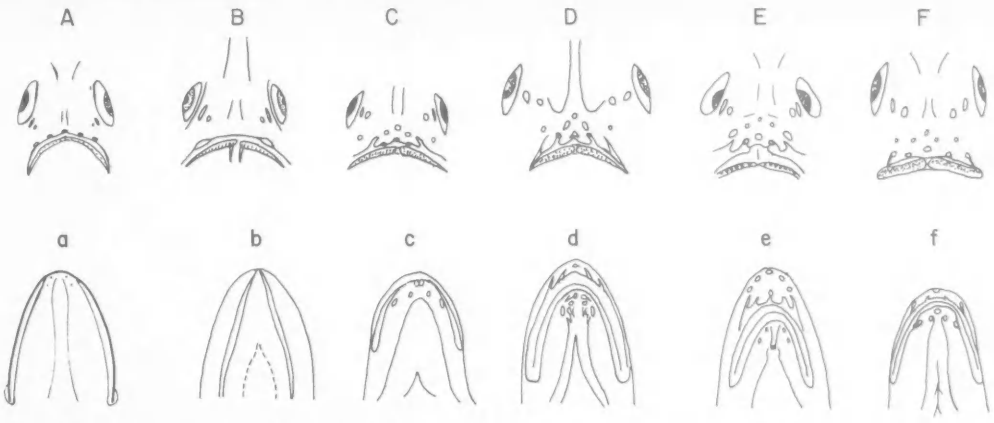

FIGURE 26.—Anterior view of snout (captial letters) and ventral view of lower jaw (lower case letters) in juveniles of six species of sciaenids: A, a, *Larimus fasciatus*; B, b, *Cynoscion regalis*; C, c, *Bairdiella chrysoura*; D, d, *Micropogonias undulatus*; E, e, *Menticirrhus saxatilis*; F, f, *Leiostomus xanthurus*.

pores plus six minute barbels at the tip of the lower jaw (Figure 26D, d). *Menticirrhus saxatilis* has five marginal pores and three upper pores on the snout, and four mental pores and a short, rigid barbel at the tip of the lower jaw (Figure 26E, e). An apical pore is also present on the barbel of *M. saxatilis*. The anterior margin of the snout (rostral fold) in *Larimus fasciatus* and *C. regalis* is complete without notches (Figure 26A, B). *Bairdiella chrysoura* and *Leiostomus xanthurus* have a slightly indented rostral fold (Figure 26C, F), although the former has a terminal mouth and the latter has an inferior mouth (Figure 26c, f). Both *M. saxatilis* and *Micropogonias undulatus* have deeply notched rostral folds (Figure 26D, E), correlated with their inferior mouth positions. The mental pores of *Larimus fasciatus* (Figure 26a) are the smallest of these sciaenids. The barbels of *M. undulatus* and *Menticirrhus saxatilis* may differ in function as well as in number, because the single barbel of *M. saxatilis* has a pore at the tip, whereas barbels of *Micropogonias undulatus* do not (Figure 26d, e). The numbers and size of pores increase from species to species as the feeding niche tends toward the bottom; barbels are present only in the bottom feeders.

Nares

Sciaenid fishes have two pairs of closely set nostrils. The anterior one is usually round; the posterior one is oval and elongate (Figure 27). A flap of skin is sometimes also present along the posterior margin of the anterior nostril in bottom feeding species. The nasal cavity is generally oval shaped with a cluster of olfactory laminae forming a nasal rosette anteriorly. *Larimus fasciatus* has the shortest nasal cavity from anterior to posterior nostril (Figure 27A), and *Leiostomus xanthurus* has the longest (Figure 27F). The shape of the nasal rosettes and olfactory laminae are similar in these six species of sciaenid fishes. The mean number of laminae (averaging both sides per specimen and rounding upwards) differs among these species (Table 9) and is variable within a species. The numbers of laminae are 11 to 14 in *Larimus fasciatus*; 12 to 22 in *C. regalis*; 12 to 25 in *B. chrysoura*; 10 to 31 in *M. undulatus*; 11 to 22 in *Menticirrhus saxatilis*; and 16 to 30 in *Leiostomus xanthurus*. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* average fewer laminae than *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis* (Table 9). Within a species, the number of nasal laminae seems higher in larger specimens. The maximum number of nasal laminae tends to be greater in bottom feeding fishes.

Other Morphological Characters

Differences in body shape, mouth structure, food specialization, and habitat preferences of fishes may act to restrict interspecific competition within a fauna (Keast and Webb 1966). The six species of sciaenid fishes discussed here show a

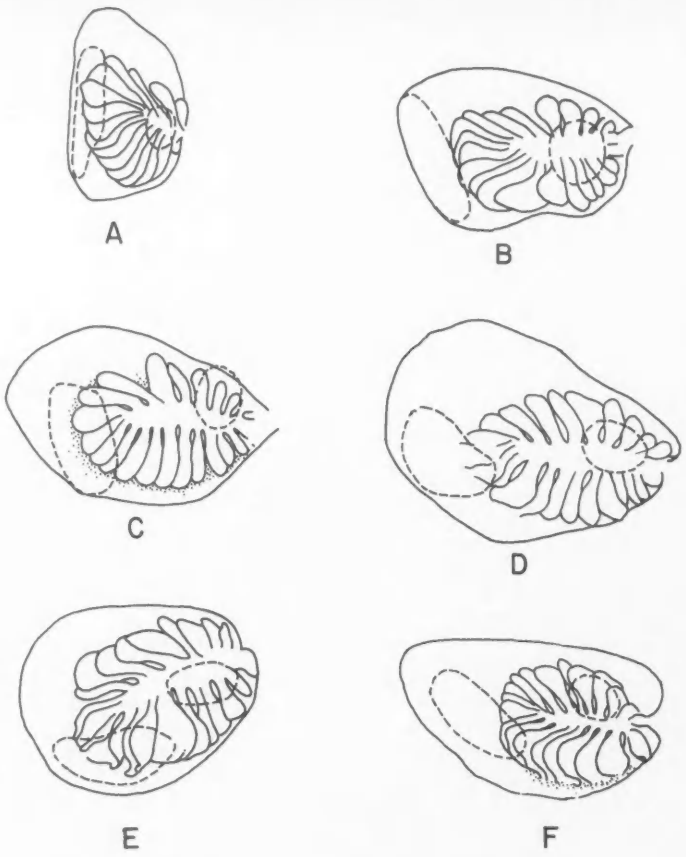

FIGURE 27.—Right olfactory rosette and nasal cavity in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Dotted circles represent nostrils, the anterior nostril to the right.

TABLE 9.—Number of laminae in olfactory rosettes in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	*N*	$\bar{x}$
Larimus fasciatus (55.3-107)		3	5	2	5																		15	12.6
Cynoscion regalis (35.2-86.4)			1	6	6	4	7	5	1	2	1	1	2										36	15.9
Bairdiella chrysoura (30.0-75.3)			2	2	2	8	4	6	2	6	3	—	—	1	—	1							37	16.8
Micropogonias undulatus (35.5-116)	1	1	—	—	3	3	4	3	3	—	2	1	2	3	2	—	2	1	1	1		1	34	19.5
Menticirrhus saxatilis (29.2-99.6)		1	—	—	1	6	6	3	3	6	3	2	1										32	17.3
Leiostomus xanthurus (47.4-148)							1	2	4	4	3	2	7	6	—	1	5	1	—	—	1		37	21.7

correlation between body shape and feeding habitat (Figure 28). Young *Larimus fasciatus* are oblong, relatively deep, and have a compressed body and a double truncate tail (Figure 28A). These features, in combination with a strong oblique mouth and large eyes (Figure 20A, A′; Table 5), indicate that *L. fasciatus* is a moderate swimmer that feeds in the upper water column by sight. Young *C. regalis* have a more fusiform and compressed body, and a long pointed tail (Figure 28B). These features, in combination with a large lique mouth and relatively large eyes (Figure 20B, 20B, B′; Table 5), indicate that *C. regalis* is a fast swimmer that feeds in the upper to middle water column by sight. Young *B. chrysoura* have an oblong and compressed body, and a broad and

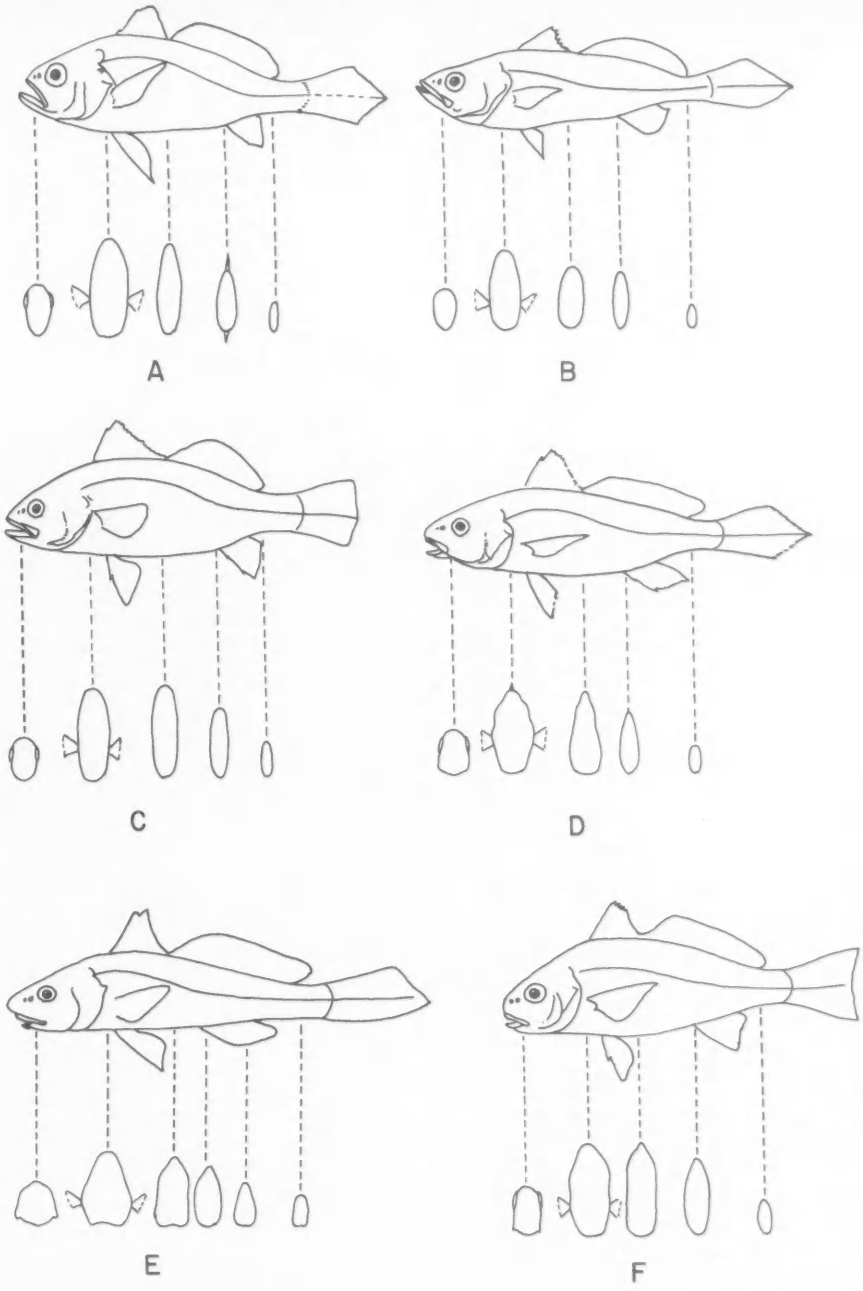

FIGURE 28.—Body shape and cross sections in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

slightly rounded to truncate tail (Figure 28C). These features, together with its terminal mouth and relatively large eyes (Figure 20C, C′; Table 5), indicate that *B. chrysoura* is a moderately fast swimmer that feeds in the middle water column by sight. Young *Micropogonias undulatus* have an elongate and less compressed body and a long pointed tail (Figure 28D). These features, combined with an inferior mouth with barbels and relatively smaller eyes (Figure 20D, D′; Table 5), indicate that *M. undulatus* is a moderately fast swimmer that feeds in the lower water column by sight, olfaction, and touch. Young *Leiostomus xanthurus* have a rather short and deep body, and a broad and truncate tail (Figure 28F). These features, combined with an inferior mouth and large eyes (Figure 20F, F′; Table 5), indicate that *L. xanthurus* is a slow swimmer that feeds in the lower water column by sight and olfaction. Young *Menticirrhus saxatilis* have an elongate, round, and narrow body, and a relatively pointed tail (Figure 28E). These features, combined with an inferior mouth with a pored-barbel (Figure 26e) and relatively smaller eyes (Figure 20E, E′; Table 5), indicate that *M. saxatilis* is a slow swimmer that feeds in the lower water column by olfaction and touch.

The cross sections of these young sciaenid fishes (Figure 28) also reflect their habitat. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* are compressed and have relatively narrow ventral surfaces (Figure 28A–C) in comparison to *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* (Figure 27D–F). Some of these morphological characters, such as the shape of the tails and the size of the eyes, vary ontogenetically. Generally, most juvenile sciaenids have pointed tails and relatively larger eyes than adults.

Food Specialization

The food habits of young sciaenids have been studied by numerous authors and the information reported by them is scattered and presented in different ways. Some of this work has been summarized for comparison with the present study (Tables 10–14). Only those studies having some sort of quantitative analysis were chosen for the comparison. Different authors have used different taxonomic categories to analyze their information. The classification of the food items in the present study has been modified from Darnell (1961) and Qasim (1972). Six major food groups were employed more or less according to their vertical occurrence in the water column, from the upper water column to the bottom. They were fishes, macrozooplankton, microzooplankton, epibenthos, infauna, and other organic matter. Within each food group, several items were listed and the generic and specific names of the primary prey species in the study area were indicated. Boundaries for these six food groups are not definite because some prey taxa move vertically in the water column and some taxa may also include both pelagic and benthic species. Generalized terms used by many authors such as shrimps, annelids, mollusks, crabs, etc., were placed under respective food groups for the convenience of comparison. Food habits of each species were compared with previous studies from different geographic areas and seasons. Food items were listed in different categories for each species. Under each listed item, there were cases where more than a single food taxon was listed by the original authors. Then, the one that had the highest frequency (by occurrence, volume, or weight) was chosen to represent that item.

All fish specimens used for stomach analyses in this study were randomly selected from specimens collected in June to November (1972 to 1974). During this period, these sciaenids reach their maximum abundance and degree of sympatry. All specimens were young-of-the-year or yearlings.

Larimus fasciatus

Stomachs of 12 *L. fasciatus* (14–125 mm TL) were examined. All stomachs contained crustaceans, exclusively: *Neomysis americana* in seven stomachs, Cumacea in five, Amphipoda (mostly *Gammarus* spp.) in four, and calanoid copepoda (mostly *Acartia tonsa*) in two. Most of these prey species were of small size.

Published information on the food habits of *L. fasciatus* was scarce. Welsh and Breder (1923) reported on food of four *L. fasciatus* (50–110 mm SL) from Mississippi and Texas. Only two stomachs had food, one with a post-larval clupeoid and the other with "schizopodous forms" (crustacean remains).

Cynoscion regalis

Stomachs of 36 *C. regalis* (67–183 mm TL) were examined (Table 10). They fed mostly on *Anchoa mitchilli* and *N. americana*. *Anchoa mitchilli* was very abundant in the same area as *C. regalis* in the

TABLE 10.—Stomach contents of weakfish, *Cynoscion regalis*, from different estuarine areas along U.S. Atlantic coast.

Author	Chao 1976	Welsh and Breder 1923				Merriner 1975	
Locality	York River, Va.	Acushnet River, Mass.	Cape Charles, Va.	Winyah Bay, S.C.	Fernandina, Fla.	Pamlico Sound and Morehead City, N.C.	
Period	June -Aug. 1973	Sept. 1882	Sept. 1916	July 1915	Mar. 1920	June 1967-Jan. 1970	
Source	Original	p. 159	p. 160	p. 161	p. 161	Table 1	
Number of specimens	36	28	45	34	105	2,159	
Empty stomachs	2	5	0	5	74	1,342	
Length of specimens	70-183 mm TL	7-11 cm SL	43-11.5 cm SL	2.8-6.2 cm SL	5-17 cm SL	135-481 mm SL	
Quantitative method	% of occurrence	% of volume	% of volume	% of volume	% of volume	% of occurrence	% of volume
Fishes:							
Anchoa mitchilli	72.2					58.1	15.6
Others and remains	8.3	48.0	2.0	9	18	15.7	74.0
Macrozooplankton:							
Mysidace	2.8						
Neomysis americana	63.9					31.0	0.9
Isopoda		0.5		6			
Decapoda (shrimps)		47.0	0.5		46	0.1	
Others and remains			91.0	83	18	1.5	1.2
Microzooplankton:							
Copepoda			3.5	2			
Epibenthos:							
Polychaeta		0.5				0.5	
Amphipoda			3.0				0.1
Others and remains						1.5	
Unidentified remains	5.6	4.0			18	96.8	8.2

Author	Thomas 1971					Stickney et al. 1975	
Locality	Delaware River, Del.					Savannah River and Ossabaw Sound, Ga.	
Period	June 1969	July 1969	Aug. 1969	Sept. 1969	Oct. 1969	May 1972-July 1973	
Source	Table 20	Table 20	Table 20	Table 20	Table 20	Table 1	
Number of specimens	71	94	94	120	66	120	
Empty stomachs	10	11	10	18	12	35	
Length of specimens	11-76 mm TL	5-123 mm TL	15-180 mm TL	20-180 mm TL	61-180 mm TL	30-169 mm SL	
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of occurrence	% of occurrence	% of occurrence	
Fishes	[1]7.0	[1]14.9	[1]16.0	[1]33.3	[1]34.8		
Anchoa mitchilli	1.4	2.1	1.1	3.3	4.5	2.5	
Others and remains	2.8	7.4	13.8	12.5	30.3	31.7	
Macrozooplankton:							
Mysidace	74.6	59.6	65.8	66.7		0.8	
Neomysis americana						55.0	
Isopoda		4.3	2.1	1.7		2.5	
Decapoda (shrimps)		2.1	3.2	6.7	10.6	2.5	
Others and remains							
Microzooplankton:							
Copepoda	19.7	4.3	2.1	3.3		5.0	
Calanoid						2.5	
Others and remains	9.9	4.3	1.1	0.8	1.5		
Epibenthos:							
Neris succinea						15.0	
Amphipoda						2.5	
Gammarus sp.	9.9	58.5	58.5	28.3	28.8	1.7	
Others and remains						9.2	
Unidentified remains						2.5	

[1]All fishes combined.

same months (Colvocoresses 1975; Markle 1976). Fishes and planktonic crustaceans were the major food items of *C. regalis* (Table 10). A shift of food habits with growth was noted by Thomas (1971), Merriner (1975), and Stickney et al. (1975). The smaller weakfish fed more on mysid shrimp and the larger weakfish fed more on fishes.

Bairdiella chrysoura

Stomachs of 68 *B. chrysoura* (57–190 mm TL) were examined (Table 11). They fed mainly on *N. americanus* and *A. mitchilli*. In other areas, juvenile *B. chrysoura* fed mainly on crustaceans and fishes (Table 11). Smaller specimens (<40 mm SL) fed mostly on copepods but as they grew they fed more on *N. americanus*, amphipods, and other larger crustaceans. Fishes became more important food items for specimens over 70 mm SL (Thomas 1971; Carr and Adams 1973; Stickney et al. 1975).

Micropogonias undulatus

Stomachs of 69 *M. undulatus* (65–199 mm TL) were examined (Table 12). They showed as wide a variety of prey items as have previous studies from other geographic areas (Table 12). Polychaetes

TABLE 11.—Stomach contents of silver perch, *Bairdiella chrysoura*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Chao 1976	Thomas 1971	Welsh and Breder 1923
Locality	York River, Va.	Delaware River, Del.	Cape Charles, Va.
Period	June-Aug. 1973	Aug.-Oct. 1969	Sept. 1916
Source	Original	Table 45	p. 174-175
Number of specimens	68	99	21
Empty stomachs	10	9	0
Length of specimens	57-153 mm TL	5-130 mm TL	6-8.2 cm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence
Fishes		[1]12.1	
Anchoa mitchilli	5.1	3.0	
Others and remains	20.7	8.1	1
Macrozooplankton:			
Mysidace	1.7	89.9	
Neomysis americana	74.1		
Isopoda	1.7	1.0	
Decapoda (shrimp)	10.3	17.2	5
Others and remains	1.7		87
Epibenthos:			
Annelida (polychaete)	3.5		2
Neris succinea	3.5		
Cumacea	1.7		
Amphipoda	1.7	15.2	5
Gammarus sp.	3.5	62.6	
Crabs		3.0	
Others and remains	1.7		
Infauna (bivalve and Nematoda)	3.5		
Unidentified remains	6.9	2.0	

Author	Stickney et al. 1975	Reid, 1954		Carr and Adams 1973
Locality	Savannah River and Ossabaw Sound, Ga.	Cedar Key, Fla.		Crystal River, Fla.
Period	May 1972-July 1973	June 1950-May 1951		Oct. 1970-Aug. 1971
Source	Table 1	Table 5		Estimate from Fig. 9
Number of specimens	161	45	6	195
Empty stomachs	45	0	0	43
Length of specimens	30-149 mm TL	25-99 mm SL	100-130 mm SL	5-130 mm TL
Quantitative method	% of occurrence	% of occurrence		% of occurrence
Fishes:				
Anchoa mitchilli	2.7			
Others and remains	6.6	4.4	16.6	31.2
Macrozooplankton:				
Mysidace	0.6			
Neomysis americana	25.1			
Isopoda	1.1			
Decapoda (shrimp)	5.5	73.3	33.3	51.6
Others and remains	8.2	4.4	66.6	
Microzooplankton				
Copepoda	3.9	4.0		
Others and remains	2.2			
Epibenthos:				
Annelida (polychaete)	0.6	2.2		7.3
Neris succinea	8.2			
Amphipoda	2.2	33.3	16.6	9.2
Gammarus sp.	6.0			
Crabs	8.2		16.6	
Others and remains	0.6	6.6		
Unidentified remains				8

[1]All fishes combined.

and crustaceans were the main food items of the juvenile *M. undulatus* in the study area. Juvenile *M. undulatus* fed on a large variety of invertebrates and sometimes fishes (Table 12). Stickney et al. (1975) indicated that smaller specimens (<100 mm SL) depend extensively on harpacticoid copepods, which are mainly bottom dwellers. As the fish grow, they become more generalized feeders (Parker 1971). Geographic variation in food habits of juvenile *M. undulatus* (Table 12) probably is attributable to availability of prey species in the area.

Menticirrhus saxatilis

Stomachs of 20 *M. saxatilis* (36.5–118 mm TL) were examined. All contained crustaceans and polychaetes were also important in their diet. The occurrence of organic detritus was also frequent suggesting that *M. saxatilis* is a bottom feeder. The literature also indicates that juvenile *M. saxatilis* feed mainly on crustaceans and polychaetes (Table 13). Welsh and Breder (1923) indicated that *M. saxatilis* fed mainly on relatively large crustaceans.

Leiostomus xanthurus

Stomachs of 77 *L. xanthurus* (73–205 mm TL) were examined. Although they showed a wide variety of food species, the major part of the food was benthic. *Pectinaria gouldii*, a burrowing polychaete, was a major food item in the diet of *L. xanthurus* in the study area. Stickney et al. (1975)

TABLE 12.—Stomach contents of croaker, *Micropogonias undulatus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Chao 1976	Thomas 1971	Roelofs 1954	Welsh and Breder 1923		Stickney et al. 1975	Hansen 1969	Parker 1971			
Locality	York River, Va.	Delaware River, Del.	North Carolina coast	Winyah Bay, S.C.	Cape Canaveral, Fla.	Savannah River and Ossabaw Sound, Ga.	Pensacola, Fla.	Lake Pontchartrain, La.		Clear Lake, Tex.	
Period	June-Aug. 1973	Nov.-Dec. 1970	All seasons 1950	July 1915	Dec. 1919	May 1972-July 1973	Aug. 1963-Dec. 1965	Jan. 1963-Dec. 1965			
Source	Original	Table 71	Table 1	p. 184	p. 183	Table 1	Table 5	Table 26			
Number of specimens	69	25	159	37	24	196	2,520	63	44	1,866	475
Empty stomachs	5	3	?	0	6	15	?	2	6	194	15
Length of specimens	56-199 mm TL	23-50 mm TL	60-140 mm TL	4.2-6.2 cm SL		39-180 mm SL	76-173 mm TL	10-74 mm TL	75-124 mm TL	10-96 mm TL	70-110 mm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of volume		% of occurrence	% of volume	% of occurrence			
Fish and remains	20.3		3.1	0.7		7.5	15.9	11	9	4	5
Macrozooplankton							[1]14.3				
Mysidace	3.1	64.0	5.7			1.0		5	4.5	2	2
Neomysis americana	35.9					16.9					
Isopoda	1.6	4.0				1.0		6.5	8.0	10.5	18.0
Decapoda (shrimp)	9.4		3.1	7.0	24.0	3.0		17.0	18.5	19.5	14.5
Insecta	1.6					0.5		3	18.5	13.0	20.0
Others and remains	3.1			7.0							
Microzooplankton:											
Copepoda	3.1	76.0	25.2			7.0		2.0	6.5	1.0	3.0
Calanoid	10.9					1.0					
Harpacticoid						10.0					
Ostracoda						0.5		8.0	12.0	9.0	8.0
Others and remains	6.3		4.4	2.0							
Epibenthos:											
Annelids (polychaetes)	67.2		89.9	29.0	3.0	12.4	61.5	17.0	6.5	6.0	7.0
Neris succinea	18.8					3.0					
Glycinde solitaria	9.4										
Phyllodocid	1.6										
Spionid	6.3					1.0					
Cumacea	4.7			2.0		6.0		4.0	4.5	5.0	16.0
Amphipoda	21.9		5.7			8.0					
Gamanarus sp.	7.9					9.5		17.0	10.0	16.0	10.5
Crabs	3.1			1.8		4.5		17.0	18.5	22.0	18.0
Others and remains	6.3			1.0	2.5	7.0					
Infauna:											
Pectinaria gouldii	15.6										
Ampharetid	1.6										
Gastropoda	1.6							[2]9.0	[2]3.0	[2]18.0	[2]18.0
Pelecypoda			11.3			2.5	[2]3.5				
Nematoda			0.6				0.3				
Unidentified remains and organic matters	23.5		4.4	22.0	48.0	35.6	2.5	17.0	14.0	12.0	9.0

[1]Arthropods.
[2]Mollusks.

TABLE 13.—Stomach contents of northern kingfish, *Menticirrhus saxatilis*, from different estuarine areas along U.S. Atlantic coast.

Author	Chao 1976	Welsh and Breder 1923	
Locality	York River, Va.	Cape May, N.J.	Falmouth, Mass.
Period	Mar. 1972-Dec. 1974	Aug. 1916	Aug. 1892
Source	Original	p. 194	p. 194
Number of specimens	20	21	17
Empty stomachs	0	0	4
Length of specimens	37-118 mm TL	1.9-7.2 cm SL	2.4-7.4 cm SL
Quantitative methods	% of occurrence	% of vol.	% of vol.
Macrozooplankton:			
Neomysis americana	35.0		
Isopoda		5.0	
Decapoda (shrimp)		9.0	42.0
Crangon septemspinosa	5.0		
Palaemonetes	10.0		
Insecta	5.0		
Others and remains	70.0	9.0	42.0
Microzooplankton:			
Copepoda	5.0		
Calanoid	5.0		
Epibenthos:			
Polychaetes	70.0	19.0	
Glycindae solitaria	10.0		
Spionids	15.0		
Amphipoda	35.0	30.0	
Gammarus sp.	15.0		
Others and remains	40.0		
Unidentified remains and organic matters	50.0	26.0	16.0

found that harpacticoid copepods were the main food for juvenile *L. xanthurus* and that seasonal variations in diet were slight. Organic detritus and unidentified remains were also common in stomachs (Table 14).

Food Partition

To compare the feeding habits of the juveniles of the six sciaenid species, a chart (Figure 29) has been prepared for the six food groups defined previously. The main food group of *Larimus fasciatus* was mostly planktonic and the primary food species was *Neomysis americana*. *Cynoscion regalis* and *B. chrysoura* fed mainly on fishes and macrozooplankton; the primary food species were *Anchoa mitchilli* and *N. americana*, respectively. *Micropogonias undulatus* fed on a wide variety of food including all six food groups, with the dominant food organisms being *N. americana* and *Nereis succinea*. *Menticirrhus saxatilis* fed mainly on macrozooplankton and epibenthos, with the primary food organisms being *N. americana* and polychaetes. *Leiostomus xanthurus* fed on a wide variety of food including five food groups. The dominant food organisms were *Pectinaria gouldii* and other polychaetes.

Neomysis americana was very abundant and available to all species of sciaenids in the study area. This shrimp migrates vertically in response to change in ambient light (Herman 1962). *Neomysis americana* is negatively phototactic. In shallow turbid water (as in the study area) during daylight it might concentrate near the bottom in the darkest sector of the vertical light gradient (Stickney et al. 1975). Because of the abundance and availability of *N. americana*, the other prey items should provide a better indication of feeding specialization. As has been repeatedly shown (Tables 10–14), most fishes were sufficiently opportunistic in their food habits to take advantage of extremely abundant prey species. All the fishes in the present study were sampled by bottom trawl during the daytime. Therefore, both prey and predators probably were dwelling close to the bottom.

Polychaetes were a major food resource for the bottom feeders (Tables 12–14), *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*. But *Micropogonias undulatus* fed more on the "crawling" species of worms (Table 12) such as *Nereis* and *Nephthys* (Barnes 1968) and *L. xanthurus* fed more on "tubiculous" or "burrowing" species of worms (Table 14), such as *Pectinaria* and *Amphitrite*. This is contradictory to the findings of Roelofs (1954) and Stickney et al. (1975). Observations of the feeding behavior of these two species in aquarium generally agreed with Roelofs (1954). But *L. xanthurus* seemed to "dive" into the bottom sand much more often than *M. undulatus*, and the depth of the dives by *L. xanthurus* was not shallower than *M. undulatus* as stated by Roelofs (1954).

Correlation of Feeding Structures and Food Habits

Larimus fasciatus and *C. regalis* have oblique mouths (Figure 20A, B) and their upper jaws are slightly or not protrusible (Figure 21A, B). These features allow them to feed anteriorly and dorsally to the longitudinal axis of their bodies along their swimming course. Their mouths open as the lower jaws drop anteroventrally and the distal ends of the premaxillae move forward (Figure 20A′, B′). The mouth openings of *L. fasciatus* and *C. regalis* are relatively larger than in the other species studied (Table 5). The anterior views of their mouths (Figure 20a, a′, b, b′) show that the upper jaws (premaxillae) are longer or equal to the lower jaws (dentaries). Although both of them feed "anterodorsally" and pelagically, they did show differences in diet (Figure 29). The following mor-

TABLE 14.—Stomach contents of spot, *Leiostomus xanthurus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Chao 1976	Roelofs 1954	Stickney et al. 1975	Welsh and Breder 1923	Townsend 1956	Parker 1971	
Locality	York River, Va.	North Carolina	Savannah River and Ossabaw Sound, Ga.	St. Vincent Sound, Fla.	Alligator Harbor, Fla.	Lake Pontchartrain, La.	Clear Lake, Tex.
Period	June-Aug. 1973	All seasons 1950?	May 1972-July 1973	Apr. 1915	June 1955-May 1956	July 1959-Mar. 1961	
Source	Original	Table 1	Table 1	p. 179	Table 3	Table 13	
Number of specimens	77	73	126	50	45	22	457
Empty stomachs	4	0	7	0	9	4	60
Length of specimens	73-202 mm TL	60-140 mm TL	50-149 mm SL	2.1-3.5 cm SL	16-163 mm SL	40-99 mm TL	18-99 mm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of volume	% of occurrence	% of occurrence	
Fish & remains	8.2	6.8	5.0		11.1	19	14
Macrozooplankton:							
Mysidace	8.2	4.1				14.5	8.5
Neomysis americana	27.4	7.4					
Isopoda	2.7					7.0	16.0
Decapoda (shrimp)	1.4	5.5	0.8		5.5	19.0	15.0
Insecta	2.7	1.4	1.7			14.0	19.0
Others and remains	1.4		0.8				
Microzooplankton:							
Copepoda	21.9	100		8.0	66.7	3.0	1.0
Cyclopoid	19.2						
Calanoid	13.7		33.1				
Harpacticoid	20.5		88.4				
Ostracoda		2.7	5.8	72.0	2.8	5.0	3.0
Others and remains	1.4	6.8	7.4	1.0		14.5	13.0
Epibenthos:							
Annelids (polychaete)	56.6	32.9	11.6	1.0		14.5	13.0
Neris succinea	27.4		9.1				
Glycinde solitaria	37.0						
Nephthys sp.	11.0						
Phyllodocid	6.8						
Spionid	6.8						
Oligochaete	4.1		1.7				
Cumacea	21.9		13.2				
Amphipoda	24.7			2.0		7.0	8.5
Gammarus sp.	12.3		11.6		16.7		
Crabs	1.4						
Cnidaria	9.6						
Others and remains	5.5	13.7	2.5	0.5	16.6	19.0	12.0
Infauna:							
Pectinaria gouldii	53.4						
Ampharetid	19.2						
Gastropoda	20.5		0.8			4.0	17.0
Pelecypoda	27.4	11.0				1.5	10.0
Nematoda	34.2	71.2			30.6		
Others and remains	5.5		5.0				
Unidentified remains and organic matters	42.5	23.3	35.6	14.0	36.1	14.5	7.0

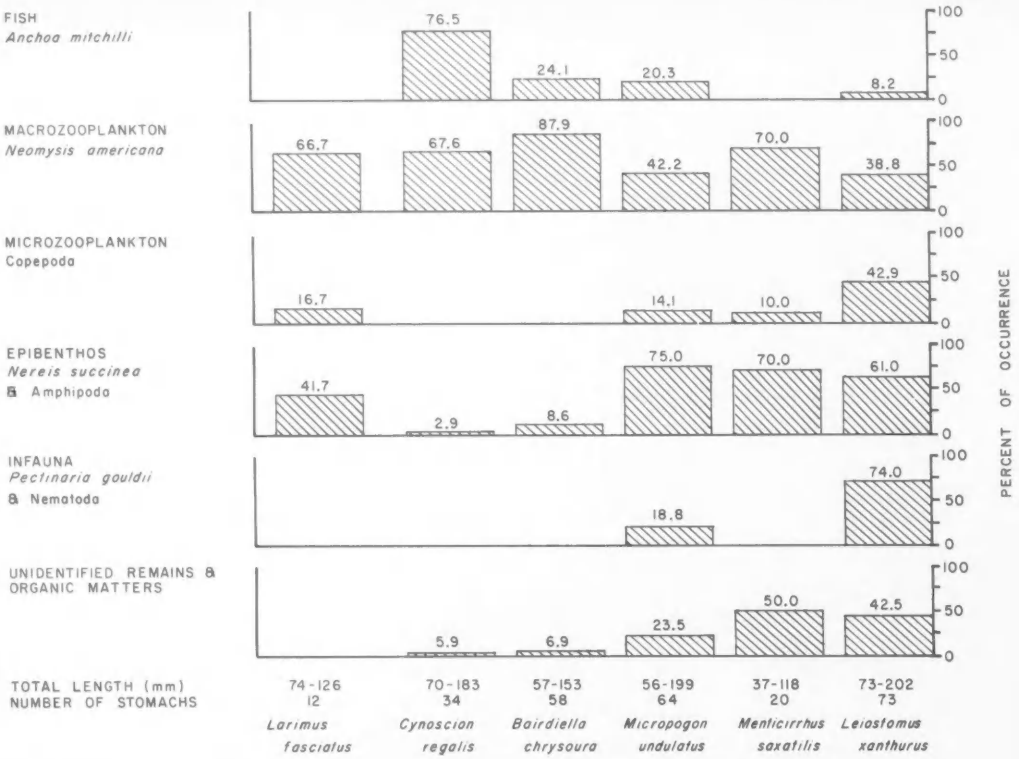

FIGURE 29.—Frequencies of occurence of various categories of food groups in stomachs of juveniles of six species of sciaenids from the York River and lower Chesapeake Bay estuary.

phological characters are correlated with the dietary differences. The premaxillary and dentary teeth of both species are sharp and set in narrow ridges or bands (Figure 22A, B). *Cynoscion regalis* has much larger teeth than *L. fasciatus*, especially a pair of large canines at the tip of upper jaw in *C. regalis*. These large sharp teeth are adaptations for grasping larger swimming prey. Both species have small sharp pharyngeal teeth (Figure 23A, B). The arrangement and size of the gill rakers (Figure 24A, B) in *L. fasciatus* are much denser and longer than those of *C. regalis*. These differences reflect the food contents in the stomachs of *L. fasciatus*, which consisted of small crustaceans collected by filtering. The stomach contents of *C. regalis* consisted of large crustaceans and fishes (Table 10). *Larimus fasciatus* has a much longer two-looped intestine than the straight intestine of *C. regalis* (Figure 25A, B; Table 7). The number of pyloric caeca in *L. fasciatus* (10 or 11) is also higher than in *C. regalis* (4 or 5). These morphological differences are probably correlated with the size of food ingested. The cephalic pore systems of *C. regalis* and *L. fasciatus* are not well developed. *Cynoscion regalis* has only two marginal pores on the snout (Figure 26B) whereas *L. fasciatus* has five minute marginal pores on the snout and four pores on the underside of the lower jaw (Figure 26A). In addition, the more fusiform *C. regalis* (Figure 28B) is adapted for fast swimming and active predation. The robust, and presumably slower moving, *L. fasciatus* (Figure 28A) shows adaptations characteristic of a plankton grazing type of feeding.

Bairdiella chrysoura has a slightly oblique terminal mouth (Figure 20C) and a slightly protrusible upper jaw (Figure 20C'). These features allow the fish to feed directly in front of its body axis along its swimming course. Its mouth opens as the lower jaw drops anteroventrally and the premaxil-

lae move forward (Figure 20C′). The relative size of the mouth opening in *B. chrysoura* (Table 5) is similar to *C. regalis*. The anterior view of its mouth opening shows equal upper and lower jaws (Figure 20c, c′). Although *B. chrysoura* feeds anteriorly, a pelagic feeder, its stomach contents are similar to those of *C. regalis* (Figure 29), except for a smaller proportion of fishes. The jaw teeth of *B. chrysoura* are strong, conical, and arranged in narrow bands, but canines are absent at the tip of the premaxilla (Figure 22C). Its pharyngeal teeth are relatively stronger and blunter than in *C. regalis* (Figure 23B, C), especially along the median rows. Gill rakers of *B. chrysoura* are intermediate between *L. fasciatus* and *C. regalis* in number (Table 6) and length (Figure 24A–C). The intestine of *B. chrysoura* has two loops and its relative length and number of pyloric caeca (6–8) are also intermediate between *L. fasciatus* and *C. regalis* (Figure 25C; Tables 7, 8). These intermediate features reflect the intermediate feeding habits of *B. chrysoura* (Figure 29). In addition, the body shape of *B. chrysoura* is oblong (Figure 28C) and not fusiform as in *C. regalis*, thus resulting in slower swimming and less efficiency in capturing fishes, as reflected in the diet. The relatively well-developed cephalic pore systems of *B. chrysoura* (Figure 26C), three upper and five marginal pores on the snout and six mental pores on the tip of the lower jaw, also may indicate that *B. chrysoura* depends more on "taste" feeding lower in the water column than *L. fasciatus* and *C. regalis*.

Micropogonias undulatus, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* have inferior mouths (Figure 20D–F) and rather protrusible premaxillae (Figure 21D–F). These features enable them to feed anteriorly and ventrally to their body axis along their swimming courses. Their mouths open as the lower jaws drop ventrally backward and the premaxillae protrude anteroventrally (Figure 20D′–F′). Their mouths are relatively smaller than those of the pelagic feeders described previously (Table 5). The anterior views of their mouths (Figure 20d, d′, e, e′, f, f′) show that the upper jaws (premaxillae) are shorter or equal to the lower jaws (dentaries). Although they all feed anteroventrally and benthically, there are differences in their feeding habits (Figure 29). These differences are reflected in the structural differences in the feeding apparatus and feeding behavior among them. The jaw teeth of *M. saxatilis*, *Micropogonias undulatus*, and *L. xanthurus* are all set in bands and the outer row of teeth on the upper jaws and an inner row of teeth on the lower jaws are slightly enlarged (Figure 22D–F). The pharyngeal teeth of *M. undulatus* and *Menticirrhus saxatilis* are conical (Figure 23D, E) and the median rows are larger and blunt. *Leiostomus xanthurus* has smaller pharyngeal teeth and the median ones are molariform (Figure 23F). The gill rakers of these three bottom feeding sciaenids differ in number (Table 6) and size (Figure 24D–F). *Menticirrhus saxatilis* has the fewest and shortest gill rakers among them. *Micropogonias undulatus* has fewer but longer gill rakers than *L. xanthurus*. The inner gill rakers of *L. xanthurus* are longest (Figure 24f′) and most numerous (Table 6). This is reflected in the larger numbers of small crustaceans (e.g., copepods) ingested by *L. xanthurus* (Table 14). The relative length of intestines (Table 7) and their in situ position (Figure 25D—F) are similar among these benthic feeders. The average relative intestinal length of *M. undulatus* and *Menticirrhus saxatilis* is slightly shorter than in *L. xanthurus* (Table 7). The numbers of pyloric caeca of these bottom feeders are similar (Table 8). The cephalic pore and barbel system differ among *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*. They all have five upper and five marginal pores on the tip of snout (Figure 26D–F). *Micropogonias undulatus* and *Menticirrhus saxatilis* also have a deeply notched rostral fold. Ventrally, *Micropogonias undulatus* has five pores and six miniature barbels (Figure 26d); *Menticirrhus saxatilis* has four pores and a short rigid barbel with an apical pore (Figure 26e); *L. xanthurus* has five pores and no barbel (Figure 26f). *Menticirrhus saxatilis* also has the most pronounced snout and most elongate and rounded body form (Figure 28E). *Leiostomus xanthurus* has the least pronounced snout and shortest and deepest body form (Figure 28F). *Micropogonias undulatus* is intermediate in snout and body form between *Menticirrhus saxatilis* and *L. xanthurus*.

The length of snout and body form reflect the feeding habits of these three species. Food habits (Figure 29) indicate that *M. saxatilis* and *Micropogonias undulatus* feed on the substrate, on the epifauna, more than they feed "into" the substrate on the infauna. *Leiostomus xanthurus* feeds more on the infauna. The long projecting snout seems to be an obstacle for fishes with an inferior mouth to forage into the bottom for food. Roelofs' (1954) observations on feeding behavior of *M. undulatus* and *L. xanthurus* in aquaria with sandy bottoms were repeated during the present study. Juveniles

of both species foraged into the bottom sand often, especially when the substrate was freshly dug from the beach. Foraging tapered off gradually, especially in *M. undulatus*, apparently as the food in the substrate decreased. Brine shrimp, *Artemia*, were fed to these two species in the aquarium. Both *M. undulatus* and *L. xanthurus* were able to feed on brine shrimp just below the water surface. *Micropogonias undulatus* fed on the surface shrimp in an oblique to vertical position. To feed on brine shrimp close to the surface, *L. xanthurus* occasionally maneuvered in an oblique upside-down position, with the dorsal fin pointing toward the bottom to overcome the inferior position of its mouth.

Other accessory organs of feeding, such as the nares and eyes, also reflect the feeding habits of young sciaenid fishes. The numbers of nasal laminae of the six species (Table 9) overlap, partly due to ontogenetic changes; the absolute numbers of nasal laminae increase as the fishes grow larger. Generally, the bottom feeders, *M. undulatus* and *L. xanthurus*, have more nasal laminae than *Larimus fasciatus, C. regalis,* and *B. chrysoura* (Table 9). *Menticirrhus saxatilis* has relatively fewer nasal laminae than other benthic feeders, but it has a pored mental barbel on the lower jaw. This suggests that *M. saxatilis* depends more on touch for foraging than other benthic feeders. The relative eye size of *M. saxatilis* is smaller than in other sciaenid fishes studied here (Table 5). Larger eyes were found among the pelagic feeders, *L. fasciatus, C. regalis,* and *B. chrysoura* (Table 5). Allometrically, the relative eye size of all these sciaenid fishes is larger in young specimens and smaller in adults. For benthic feeders, decrease in relative eye size with growth is faster than for the pelagic feeders. The relative roles of olfaction, touch, and vision in feeding in young sciaenids studied may be hypothesized as follows. The benthic feeders, *Micropogonias undulatus, L. xanthurus,* and *Menticirrhus saxatilis*, depend more on their senses of smell or touch or both to locate their prey. The pelagic feeders, *Larimus fasciatus, C. regalis,* and *B. chrysoura,* depend more on sight to catch their prey, especially *C. regalis* and *B. chrysoura* which prey on *Anchoa mitchilli*, an active small anchovy.

Morphological differences in the feeding apparatus, especially the mouth position, size, and protrusibility, the form of teeth, and the gill raker structure are limiting factors for the level of water column and the size of the prey species which can be eaten by the fish. The pelagic feeders, *L. fasciatus, C. regalis,* and *B. chrysoura*, almost completely lack any sedentary benthos in their diets (Figure 29). Even among the bottom feeders, *Micropogonias undulatus* feeds more on epibenthic polychaete species (Table 12) and *Leiostomus xanthurus* feeds more on burrowing polychaete species (Table 14).

Morphological differences in the digestive tract, the number of pyloric caeca, and the length of intestine may be adaptations to more efficient use of food. As is evident in *Larimus fasciatus* and *Leiostomus xanthurus*, size of the food items is important; *Larimus fasciatus* fed exclusively on small crustaceans (small Mysidacea and Amphipoda), *Leiostomus xanthurus* fed mainly on copepods (Table 14). *Larimus fasciatus* is mainly a pelagic feeder and *Leiostomus xanthurus* is mainly a benthic feeder. Both species have longer intestines (Table 7) and more pyloric caeca (Table 8) than other species in their respective groups (pelagic and benthic).

Svetovidov reported a similar relationship between the number of gill rakers and size of food items in Caspian shads (Nikolsky 1963). However, he also found more pyloric caeca in shad that fed on fishes than in species that ate small crustaceans, a relationship opposite to that found here. In feeding, the role of gill rakers is in ingestion and the role of the pyloric caeca is in digestion. Although there are morphological and numerical correlations among the ingestive apparatuses and digestive organs, they are highly adaptive and may be variable among fishes.

The so-called "selective feeding habits" of these young sciaenids reported by many previous authors (see citations of Tables 10–14) are not evident in the present study. Partitioning of food among these young sciaenids depends more on the habits of the prey species than on "selective preferences" of the fishes. Juvenile sciaenids feed opportunistically in a limited depth range in the water column, probably within or close to 2 m above the bottom. Within this layer of the water column, *Larimus fasciatus, C. regalis,* and *B. chrysoura* feed in the upper portion of the water column and *M. undulatus, Leiostomus xanthurus,* and *Menticirrhus saxatilis* feed in the lower portion of the water column to the bottom. Feeding niche division and resulting dietary differences among these species of sciaenids in the Chesapeake estuary area are probably attributable to differences in feeding behavior imposed

upon these species by adaptive morphological limitations rather than to selective feeding per se.

CONCLUSION

In the Sciaenidae, a family of primarily coastal marine fishes, many species utilize the same coastal area as common nursery and seasonal feeding grounds. In the York River estuarine system, the coexistence of sciaenid fishes may be attributed to: 1) Differences in their temporal and spatial distributions. Juveniles of the four most abundant sciaenid fishes entered the estuary at different times of the year. Within a given period, the highest catches of each species were usually in different areas (upper and lower reaches) and depths (beach zone, shoals, and channel) of the York River system. Also, the size distributions of each species were often separated temporally and spatially. 2) Differences in their habitat adaptations and food habits. The diverse morphological features of these sciaenid fishes enable them to utilize food resources from different levels (microhabitats) of the water column. Correlations of feeding apparatus, digestive system, and food habits are evident and result in niche division. 3) The abundant food resources of the study area. At times some prey organism (e.g., *Neomysis americanus*) may be ubiquitous and very abundant, providing food for several species of juvenile sciaenids. Then food would not be a limiting resource and intrafamilial competition may not occur.

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THE UNITED STATES SHRIMP FISHERY OFF NORTHEASTERN SOUTH AMERICA (1972–74)[1]

ALBERT C. JONES AND ALEXANDER DRAGOVICH[2]

ABSTRACT

The Guianas–Brazil shrimp fishery off the northeastern coast of South America is supported by four principal species—pink-spotted shrimp, *Penaeus brasiliensis;* brown shrimp, *P. subtilis;* pink shrimp, *P. notialis;* and white shrimp, *P. schmitti*. The areas off Guyana, Surinam, and western French Guiana were dominated by pink-spotted shrimp; brown shrimp were most prevalent off eastern French Guiana and Brazil, pink shrimp off Guyana, and white shrimp off Guyana, French Guiana, and Brazil, chiefly in shallow waters.

U.S.-flag vessels landed 5.0 million pounds of shrimp during the second half of 1972, 13.6 million pounds in 1973, and 9.0 million pounds in 1974. In 1973 and 1974 U.S.-flag vessels took 50% and 39% of the total international landings. Mean annual catch rates for 1972, 1973, and 1974 were 20.0, 26.0, and 18.3 lb/h, respectively. Monthly catch rates peaked each year in March and April and declined gradually thereafter. The catch rates off Brazil were higher than off the Guianas. Most fishing was carried on at night and at depths of 21–35 fathoms.

Small shrimp appeared to be recruited to the fishery mainly in April and October and mainly off French Guiana, Brazil, and Guyana.

An exponential surplus yield model estimated the maximum sustainable yield to be 28.7 million pounds and a linear model estimated the maximum sustainable yield to be 27.1 million pounds. Maximum observed yield was 27.3 million pounds (1973).

The shrimp resource off the northeastern coast of South America (Figure 1) is the basis of a major international fishery. This fishery consists of four principal species—pink-spotted shrimp, *Penaeus brasiliensis;* brown shrimp, *P. subtilis;* pink shrimp, *P. notialis;* and white shrimp, *P. schmitti*. *Penaeus subtilis* and *P. notialis* until recently were known as *P. aztecus subtilis* and *P. duorarum notialis*, respectively (Pérez Farfante in press). The earliest exploratory fishery survey of the continental shelf off the northeastern coast of South America was made in 1944 by Whiteleather and Brown (1945). Commercial shrimp fishing by U.S. vessels began in 1959 stimulated by exploratory surveys made in 1957 and 1958 (Higman 1959; Bullis and Thompson 1959). Thereafter the fishery expanded rapidly and soon included vessels of other nations. The history of the fishery through 1959, and a description of the fishing grounds, species, fishing fleets, and stock status, is given by Naidu and Boerema (1972).

This report is based on data collected in 1972–74 from U.S.-flag vessels and from processing plants under the terms of the bilateral United States–Brazil Shrimp Agreement. This paper evaluates and reviews the status of the fishery based on analysis of these data. Information from processing plant records before 1972 is also used.

The United States–Brazil Shrimp Agreement of 1972 dealt with conservation of shrimp resources and operations of U.S. shrimp vessels off northern Brazil (Allen 1973). The agreement stated that the information on catch and effort, and biological data relating to the shrimp fishery in that area, be collected from U.S. vessels. Similar agreements were effected between Brazil and Barbados, Surinam, and Trinidad and Tobago.

SOURCES OF DATA AND METHODS

Catch data for U.S. vessels came from logbooks and landing records for July 1972–December 1974 (Figure 2; Appendix Table 1). Logbook records were submitted for approximately 50% of the fishing trips, but this percentage varied monthly from 10% at the beginning of data collection to 80% later in the period. Landing records were submitted for all trips. Information on area of cap-

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[2]Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

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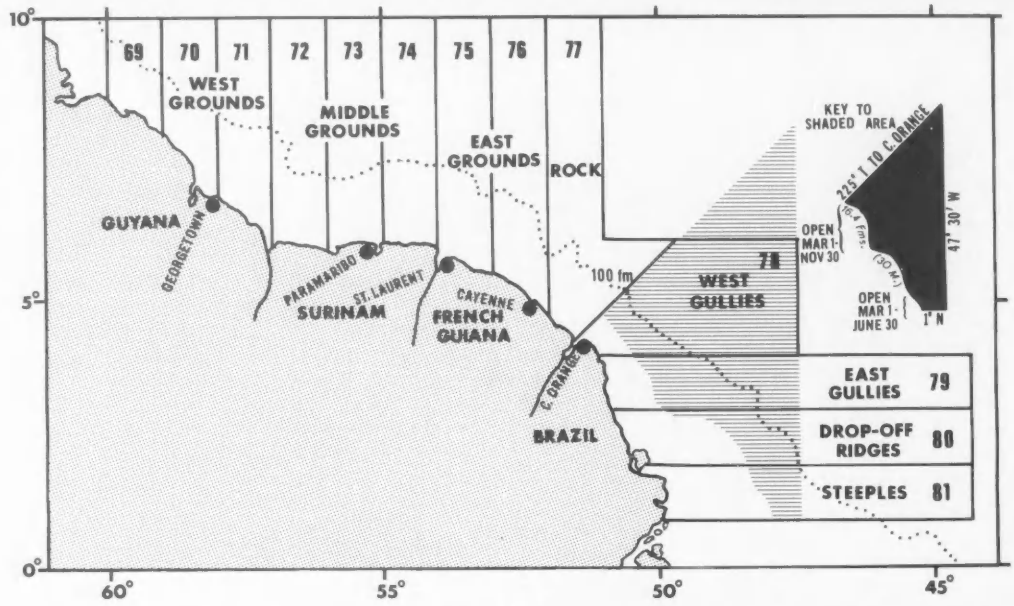

FIGURE 1.—The Guianas–Brazil shrimping grounds. The chart shows the fishing zones and their common names. The United States-Brazil Shrimp Agreement Area is shaded and the boundaries of the Area and the fishing seasons for U.S. vessels are shown in the insert.

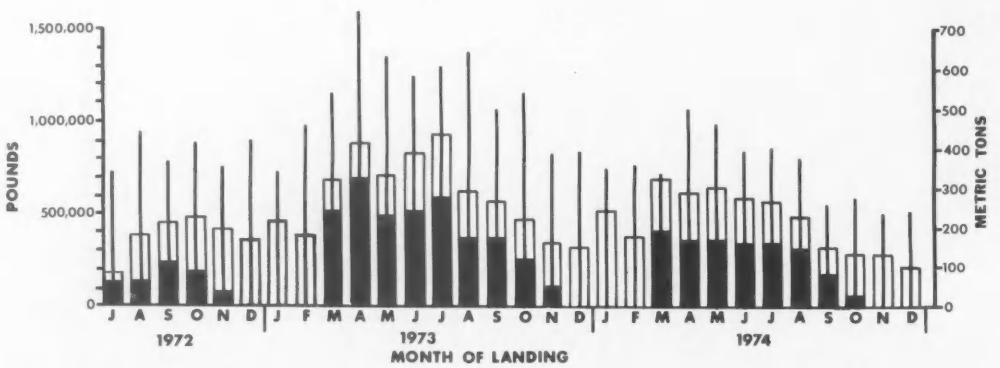

FIGURE 2.—Shrimp catches of U.S. vessels by month and area for the Guianas–Brazil fishery. Weights of heads-off shrimp are in pounds and metric tons. Vertical lines represent the total U.S. landings reported by the processing plants and are reported by month in which the landing was made. Vertical bars represent the "hail" or estimated catches of U.S. vessels submitting logbooks and are reported by the month of capture. The shaded area of the vertical bar represents the proportion of the logged catches recorded from the United States-Brazil Shrimp Agreement Area.

ture, fishing effort, catch, and species and size of shrimp, were taken from logbooks and landing records. The vessel captain made daily entries in the logbook on fishing area (identified by 1°-coastal zone and by water depth), fishing effort (number of hauls and number of hours fishing, by day and by night), estimated shrimp catch (pounds, heads-off weight), and most abundant

species, and commercial tail-weight. The retained catch was reported; no estimate was made of the discarded catch. Landing records for each fishing trip included the total weight of shrimp in each commercial weight category. The landings were recorded in two categories: "mixed" shrimp (pink-spotted, brown, and pink) and white shrimp. In our treatment of the landing data, however, we combined the landings of "mixed" and white shrimp. Information on area of catch was not available in the landing records. In addition, processing plants reported total yearly landings of shrimp and average fleet sizes, including both U.S.- and other-flag vessels.

We estimated total monthly areal catches by adjusting the monthly catches reported by area in logbooks for 1) catches unreported by area and 2) landings unreported in logbooks. For example, the total U.S. catch off northern Brazil (fishing zones 78–81) in April 1974 was estimated as follows:

$$A = A' \times \frac{B}{B'} \times \frac{C}{C'}$$

where A = estimated total catch in zones 78–81, April 1974;
A' = catch reported in logbooks for zones 78–81, April 1974;
B = total catch reported in logbooks, April 1974;
B' = total catch reported in logbooks by fishing zone, April 1974;
C = total landings reported in landing records, April and May 1974;
C' = total catch reported in logbooks, April and May 1974.

The ratio B/B' adjusted A' for the logbook catch that was unreported by fishing zone and the ratio C/C' adjusted for the landings that were unreported in logbooks. The second ratio used data for 2 mo, since catches made in a given month often were landed in both that and the following month. This method resulted in estimates of the total annual catches by areas of capture which were within 2% of the total reported annual landings. The logbook sample was not random and the catch off Brazil was probably overestimated, since more vessels probably submitted information when fishing off Brazil than when fishing off the Guianas. However, there was no way to assess the difference in completeness of reporting of vessels fishing different areas. For this reason, estimates of catches were not made for smaller subareas.

The size index was a weighted mean value calculated by assigning the values 1, . . . 9 to the commercial tail-weight categories >50, . . . <15.

ANNUAL LANDINGS AND CATCHES

During the second half of 1972, total landings by U.S.-flag vessels were 5.0 million pounds; in 1973 and 1974, they were 13.6 and 9.0 million pounds, respectively (Table 1). Landings of U.S. vessels were 50% and 39% of total international landings in 1973 and 1974. Monthly catches (Table 2) vary slightly from landings since they are estimated values and because catches are often landed in months subsequent to the month of capture.

To gain a perspective of the entire fishery, we assembled the historical landings of U.S.- and foreign-flag vessels for 1960–74 (Table 3, Figure 3) and the number of shrimp trawlers by country for 1961–74 (Table 4). There was a continuous increase in landings from 1960 (3.9 million pounds) through 1968 (27.3 million pounds). The landings declined slightly in 1969 and 1970 to 27.1 and 27.0 million pounds, respectively. There was a sharp decline in landings in 1971 and1972 (to 22 million pounds). In 1973 the fishery attained a maximum catch of 27.3 million pounds. The following year there was a decline in landings to 23.1 million pounds.

Ninety percent of the landings from 1960 through 1974 were made in Guyana (46%), French Guiana (21%), Surinam (14%), and Trinidad (10%). The remaining landings were made in Barbados (6%), Brazil (3%), and Venezuela (1%). National- and foreign-flag vessels landed in Barbados, Trinidad, Guyana, Surinam, and French

TABLE 1.—Landings of shrimp in pounds, heads-off weight, reported for U.S. vessels in the Guianas–Brazil shrimp fishery, 1972–74. This table is based on data submitted by processing plants; monthly data for January–June 1972 were not available.

Month of landing	1972	1973	1974
January		774,056	757,189
February		967,677	772,844
March		1,145,173	704,377
April		1,589,147	1,072,920
May		1,346,502	948,434
June		1,226,817	832,016
July	715,929	1,291,120	864,596
August	940,223	1,362,976	813,548
September	777,443	1,049,902	548,299
October	888,829	1,147,035	617,972
November	747,252	824,470	523,404
December	889,776	844,284	520,493
Total	4,959,452	13,569,159	8,976,092

TABLE 2.—Estimated total catch of shrimp in pounds, heads-off weight, by area of capture for U.S. vessels in the Guianas–Brazil shrimp fishery, 1972–74. Monthly data for January–June 1972 were not available.

Month of capture	1972			1973			1974		
	Zones 69–77	Zones 78–81	Total	Zones 69–77	Zones 78–81	Total	Zones 69–77	Zones 78–81	Total
January				884,040	—	884,040	924,749	—	924,749
February				943,550	—	943,550	558,397	—	558,397
March				354,064	1,028,331	1,382,395	405,853	635,532	1,041,385
April				319,021	1,214,699	1,533,720	434,842	597,420	1,032,262
May				349,367	838,737	1,188,104	415,514	497,284	912,798
June				480,020	805,609	1,285,629	352,805	448,404	801,209
July	253,057	561,134	814,191	541,619	969,059	1,510,678	337,220	566,662	904,482
August	560,547	316,461	877,008	464,255	690,750	1,155,005	240,074	502,583	742,657
September	425,187	410,184	835,371	386,446	737,912	1,124,358	269,655	266,952	536,607
October	550,666	337,679	888,345	531,989	482,733	1,014,722	428,949	114,212	543,161
November	649,768	149,558	799,326	518,332	238,878	757,210	512,751	11,956	524,707
December	713,867	—	713,867	669,802	—	669,802	318,141	—	318,141
Total	3,153,092	1,775,016	4,928,108	6,442,505	7,006,708	13,449,213	5,199,550	3,641,005	8,840,555

TABLE 3.—Annual landings of shrimp for the Guianas–Brazil shrimp fishery, 1960–74. Figures are in thousands of pounds, heads-off weight. Figures in parentheses are estimated values. Data for 1960–69 are from Naidu and Boerema (1972).

Year	Barbados	Trinidad	Venezuela	Guyana	Surinam	French Guiana	Brazil	Total
1960	—	—	—	3,568	381	—	—	3,949
1961	—	—	—	3,942	447	—	—	4,389
1962	—	—	—	5,126	1,072	—	—	6,198
1963	319	—	—	6,040	1,387	2,789	—	10,535
1964	1,481	—	—	6,984	1,709	2,961	—	13,135
1965	1,891	—	—	8,048	2,223	3,960	—	16,122
1966	2,400	2,386	—	9,546	2,943	4,668	—	21,943
1967	2,179	3,392	—	9,036	2,536	7,279	—	24,422
1968	2,570	4,280	—	9,161	3,438	7,860	—	27,309
1969	2,069	4,469	—	10,469	3,477	6,577	74	27,135
1970	1,339	4,373	—	11,807	3,534	4,867	1,137	27,057
1971	0	3,346	—	9,642	3,083	4,559	1,349	21,979
1972	0	2,082	—	10,743	3,518	4,553	(1,500)	22,396
1973	462	1,514	[1]2,454	12,000	3,949	5,442	(1,500)	27,321
1974	864	1,808	[2]NA	11,213	4,457	3,260	(1,500)	[3]23,102

[1]Novoa, D. 1974. Pesquería Venezolana en el área de las Guayanas durante 1973. Unpubl. manuscr., 14 p. FAO Governmental Consultation on Shrimp Resources in the CICAR Area, FIR: SR/74/NR-9.
[2]Not available.
[3]Does not include catch of 11 Cuban-flag trawlers.

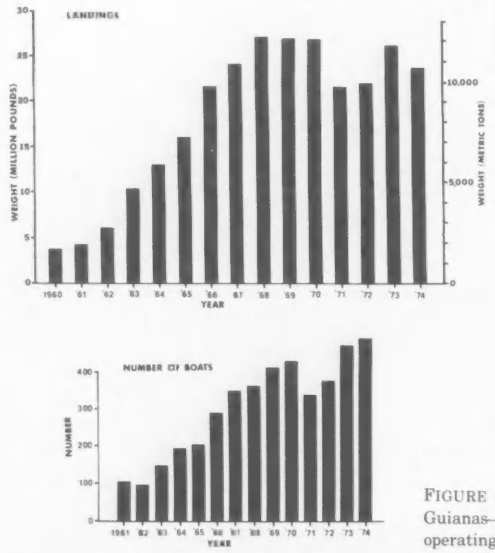

FIGURE 3.—Total landings of shrimp (heads off) for the Guianas–Brazil fishery, 1960–74 and the number of vessels operating each year. Data are from Tables 2 and 3.

Guiana; but only national-flag vessels operated in Brazil and Venezuela. The variation in landings between countries reflects mainly the differences in the sizes of the fleets supplying the processing plants in these countries (Table 3).

SPECIES COMPOSITION AND DISTRIBUTION

Our discussion about the species caught and their geographic distribution is based on data from logbooks. Vessel captains recorded a single, most abundant species to represent their daily catch; however, if two or more species were present, they recorded their catch as mixed. Single species were recorded in 58% of the catch and mixed species in 42%. Since the four species of shrimps are easily

TABLE 4.—Number of shrimp trawlers for the Guianas–Brazil shrimp fishery, 1961–74. The figures represent the average number of vessels fishing each year. Data for 1961–69 are from Naidu and Boerema (1972).

Year	Barbados	Trinidad	Venezuela	Guyana	Surinam	French Guiana (St. Laurent & Cayenne)	Brazil	Total
1961	—	—	—	60	40	—	—	100
1962	—	—	—	72	24	—	—	96
1963	—	—	—	89	25	33	—	147
1964	30	—	—	81	25	51 (20 + 31)	—	187
1965	24	—	—	96	25	58 (30 + 28)	—	203
1966	32	43	—	105	34	67 (28 + 39)	—	281
1967	32	58	—	113	50	89 (40 + 49)	—	342
1968	35	48	—	134	55	90 (53 + 37)	—	362
1969	36	63	—	142	51	110 (65 + 45)	1	403
1970	25	78	—	162	55	83 (37 + 46)	18	421
1971	—	60	—	160	45	60 (18 + 42)	21	346
1972	—	55	—	175	55	60 (17 + 43)	25	370
1973	6	42	[1]40	200	63	68 (22 + 46)	24	443
1974	21	39	[2]NA	202	106	62 (16 + 46)	30	[3]460

[1]In 1973, 50 Venezuela-flag trawlers operated for a 6-mo period.
[2]Not available.
[3]Does not include 11 Cuban-flag trawlers that fished with a mothership from March to December 1974.

distinguishable and there was no obvious bias in reporting species, we considered the single species to be representative of the entire daily catch, even though this overestimates the more abundant species. The composition of the catch for the entire area, according to this method, consisted of brown shrimp (70%), pink-spotted shrimp (23%), and other shrimps (7%) (Figure 4).

The geographic distribution of the different species of shrimps in the fishery is a subject of continuing research, but certain patterns in areal distribution were apparent (Figure 4). The areas off Guyana, Surinam, and western French Guiana (zones 69–75) were dominated by pink-spotted shrimp. Brown shrimp were listed more frequently off eastern French Guiana and Brazil (zones 76–81); white shrimp off Guyana (zones 69–71) and French Guiana and Brazil (zones 77–80); and pink shrimp off Guyana (zones 70–71).

We also examined the geographic distribution of the U.S.-vessel catch of all species. In 1972, U.S. vessels caught 36% of their catch in the Agreement Area off Brazil and 64% off the Guianas. The analogous catches for U.S. vessels in the Agreement Area were 52% (1973) and 41% (1974) (Table 2). Fishing off the Guianas (zones 69–77) was year-round. In the Agreement Area fishing by U.S. vessels was allowed 1 March–30 November (zones 78–80) and 1 March–30 June (zone 81).

Species composition of shrimp catches as reported by Japanese vessels[3] is in general agreement with our observations. Japanese catches off

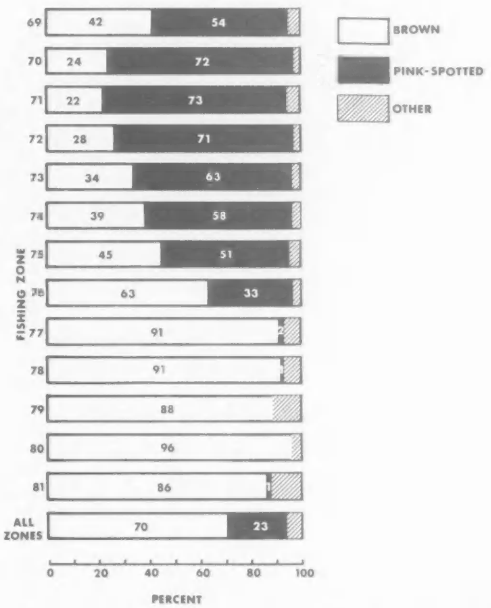

FIGURE 4.—Species composition by fishing zone of the shrimp catches of U.S. vessels in the Guianas–Brazil fishery for the period July 1972–December 1974. The data for this figure were calculated as explained in the text from the fishermen's logbooks.

Guyana and Surinam had higher percentages of "pink shrimp" (presumably mostly *P. brasiliensis*) than off French Guiana and Brazil. There were differences, however, between our data and the Japanese reports. Overall, brown shrimp were less prevalent in the Japanese catches than in the U.S. catches. The Japanese catch from 1969 to 1973

[3]Far Seas Fisheries Research Laboratory. 1971, 1972, 1973, 1974. South America north coast shrimp trawl fishing ground charts, 1969, 1970, 1971, 1972, 1973. Unpubl. manuscr., Far Seas Fish. Res. Lab., Shimizu.

was reported as 20%–35% brown shrimp (presumably *P. subtilis*) and 65%–80% pink shrimp (presumably mostly *P. brasiliensis*) (Far Seas Fisheries Research Laboratory see footnote 3).

SIZE COMPOSITION

The data on temporal and spatial distribution of sizes of shrimp provide information necessary for management of fishery stocks (Rounsefell and Everhart 1953). In particular, data on size reveal information on progressive changes as an indicator of rates of growth, population structure, maturity stages, and potential use of habitat by shrimp of different sizes, the latter being related to spawning, recruitment, and migration.

In our study the more precise data came from landing records, which we used to measure temporal changes in size composition. Size data from logbooks (less precise) were used to measure areal differences in size composition.

The majority of shrimp in U.S. landings for the entire period of 1972–74 were in the 26–30, 21–25, 16–20, and 11–15 tails-per-pound size categories (Figure 5). The sizes of shrimp caught may represent a true picture of size availability, but in many instances are also governed by factors which cause fishermen to select certain sizes (e.g., market price of shrimp, fuel price, feasibility of operation, and physical condition of the boat).

In studying the temporal and, to a lesser extent, the areal distribution of shrimp, we plotted from landing data the average size of shrimp for all ports combined and for Cayenne, French Guiana, only (Figure 6). The landings for all ports include catches from the entire fishery, while Cayenne landings reflect catches primarily off French Guiana and northern Brazil. The shrimp landed at Cayenne generally averaged slightly smaller than the shrimp from all ports combined. The smallest average size of shrimp, for both total landings and Cayenne landings, were in April and October in 1972 and 1973. In 1974, when fishing success was markedly lower than in 1973, small shrimp were present in October, but the expected April peak of small shrimp was less evident. Shrimp were larger in December–January and in June–August of each year.

Trends in average size of shrimp calculated from the logbook data were similar to those of average size calculated from the landing data (Figure 7). This similarity suggested that the size data from logbooks, although less precise, could also be used to compare areas; the smallest shrimp occurred in zones 69–70 and 77–81, and the largest in zones 71–76 (Figure 7). The magnitude of fluctuations in average size calculated from the log data were less than one size category unit, because the original data reported by fishermen are averages.

At present we have no satisfactory explanation for the greater prevalence of smaller shrimp off French Guiana and Brazil than in other areas of this fishery. We can offer some plausible hypotheses. Cayenne landings consist primarily of small brown shrimp caught off French Guiana and northern Brazil. These shrimp are probably recently recruited to the fishable population. Small

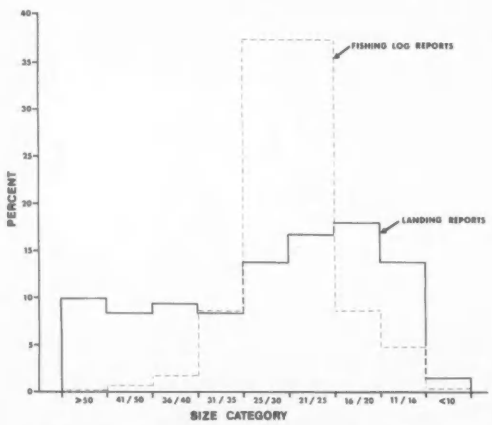

FIGURE 5.—Size composition of the shrimp catches of U.S. vessels as reported in landing records and fishing log reports for the period July 1972 to December 1974. The size categories given are the number of heads-off shrimp per pound.

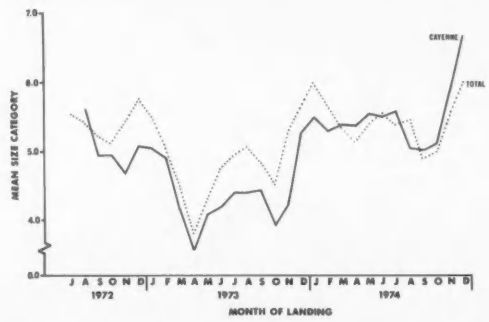

FIGURE 6.—Distribution by month of the mean size index of shrimp calculated from landing records of U.S. vessels at all ports of the Guianas shrimp fishery (marked as total on the graph) and at the Port of Cayenne, French Guiana. The size index was calculated as described in the text.

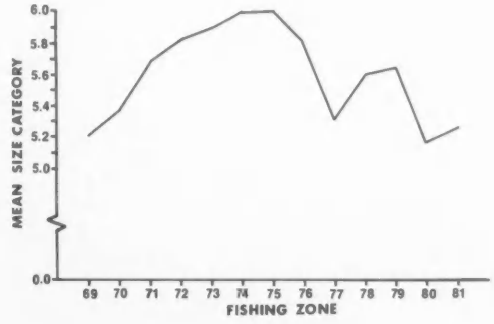

FIGURE 7.—Distribution by month and fishing zone of the mean size index of shrimp calculated from fishing log reports of U.S. vessels. The size index was calculated as described in the text.

shrimp also are present off Guyana. The smaller size of shrimp and higher catch rates in both areas, as compared with the larger shrimp and lower catch rates off Surinam, suggest that the East and West Grounds represent the principal areas of recruitment (Figure 1). Furthermore, the peaks of small shrimp in March, April, and October may indicate seasonal recruitment. Seasonal peaks in spawning and recruitment are common in penaeid shrimp populations, even where these activities occur throughout the year (Cook and Lindner 1970; Costello and Allen 1970). To determine the exact areas and chronology of recruitment for each species off the Guianas and northern Brazil will require additional research.

VARIATION IN CATCH RATES

Fishing success, or catch rate, provides a measure of the relative densities and availability of shrimp to the fishing gear and to the skilled fishermen. We examined the variations in catch rate by year, month, area, depth, and time of day to learn about the biology and ecology of the shrimp.

The average annual catch rates for U.S. vessels were 20.0 lb/fishing hour (1972 half year), 26.0 lb (1973), and 18.3 lb (1974). To observe the monthly differences in average catch rates off the Guianas and off Brazil we plotted catch rates for each statistical zone (Figures 8 and 9). Fluctuations in monthly catch rates followed a fairly regular pattern, peaking each year in March and April and then gradually declining during the remainder of the year. There were smaller peaks in July and August (Figure 8). Catch rates were consistently higher off Brazil (zones 78–81) than off the Guianas (zones 69–77). The highest catch rates were recorded in zones 78–81, intermediate in zones 75–77 and 69–71, and lowest in zones 72–74 (Figure 9).

Information on water depth without specific knowledge of the type of sediment, chemical content of water masses, and information on water temperature and speed and direction of the current means little in ecological terms. But, in a pragmatic sense, the statistics on shrimp catches versus depth are important. In our study the distribution of shrimp catches varied with water

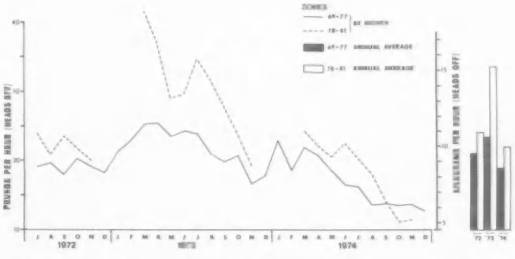

FIGURE 8.—Distribution by month of the mean catch rate of shrimp for U.S. vessels fishing off the Guianas (zones 69–77) and off Brazil (zones 78–81), July 1972 to December 1974. Catch rate is expressed as pounds and kilograms of shrimp (heads-off weight) per hour of fishing.

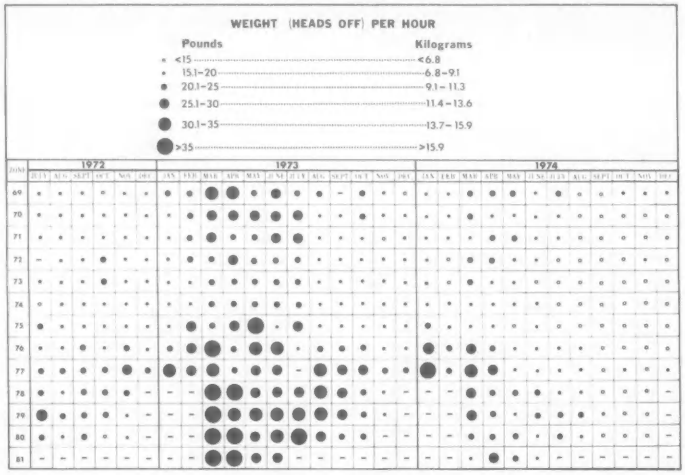

FIGURE 9.—Distribution by month and fishing zone of the mean catch rate of shrimp for U.S. vessels fishing in the Guianas–Brazil fishery, July 1972 to December 1974. See Figure 1 for location of fishing zones. Catch rate is expressed as pounds (and kilograms) of shrimp (heads-off weight) per hour of fishing.

depth. The average catch rates were: 35.4 lb/h (0–5 fm), 25.0 lb/h (6–10 fm), 21.5 lb/h (11–15 fm), 20.5 lb/h (16–20 fm), 21.1 lb/h (21–25 fm), 20.7 lb/h (26–30 fm), 21.1 lb/h (31–35 fm), 23.2 lb/h (36–40 fm), 22.7 lb/h (41–45 fm), and 24.5 lb/h (46–60 fm). Off Guyana, Surinam, and French Guiana (zones 69–77), average catches were lower at the intermediate depths (16–35 fm) than in shallower or deeper water (Figure 10). Off Brazil the average catch did not vary with depth in zones 78 and 79, but in zones 80 and 81 average catches were higher at the intermediate depths than in shallower or deeper water.

We also examined the distribution of fishing effort in relation to depth. Fishing effort was concentrated primarily in intermediate depths. Sixty percent of the fishing effort reported in logbooks occurred between 21 and 35 fm, 18% in <20 fm, and 22% in >36 fm. Off Guyana, Surinam, and French Guiana most fishing was between 16 and 30 fm; off Brazil, it was in deeper water (Figure 11). While the highest catch rates were usually in the shallow and deep zones at the edge of the fishing grounds, these areas supported only a small percentage of the total fishing effort. Shallow and deep zones probably were fished only when good catches could be made, whereas the intermediate depths were fished during times of both good and poor fishing.

The availability of shrimp to the fishermen in relation to time of day varies for each area, species, and time of the year. Most fishing for shrimp was done at night, some during the day, and some on a 24-h/day basis (Figures 12 and 13). The time spent fishing at night was three times that spent during the day. White shrimp were caught primarily during daylight hours off the Guianas and fishing in the East Gullies (zone 79) was usually done during the day. In the Drop-Off and Steeples (zones 80–81), fishing on a 24-h/day basis made up nearly half the total fishing time. The average catch rates for the entire fishery were 29.6 lb/h (day fishing), 18.9 lb/h (night fishing), and 22.1 lb/h (day and night fishing). The mean catch rates were higher for day fishing than night in all zones and at all depth intervals. We conclude that the usual strategy is to fish at night, except for certain species (e.g., white shrimp) or in certain areas (e.g., East Gullies) where day fishing is more successful. During periods of high catches, fishing is usually carried out on a 24-h/day basis until a full catch is made or until the fishermen are exhausted.

APPRAISAL OF THE FISHERY

The fishery for shrimp in the Guianas–Brazil area reached a historical maximum annual production of 27.3 million pounds heads-off in 1973. We used a surplus yield model to estimate the maximum sustainable yield of the resource (Fox 1970). We also compared predicted annual equilibrium yields with actual annual yields attained to measure the expected variation from equilibrium conditions.

An exponential surplus yield model suggested

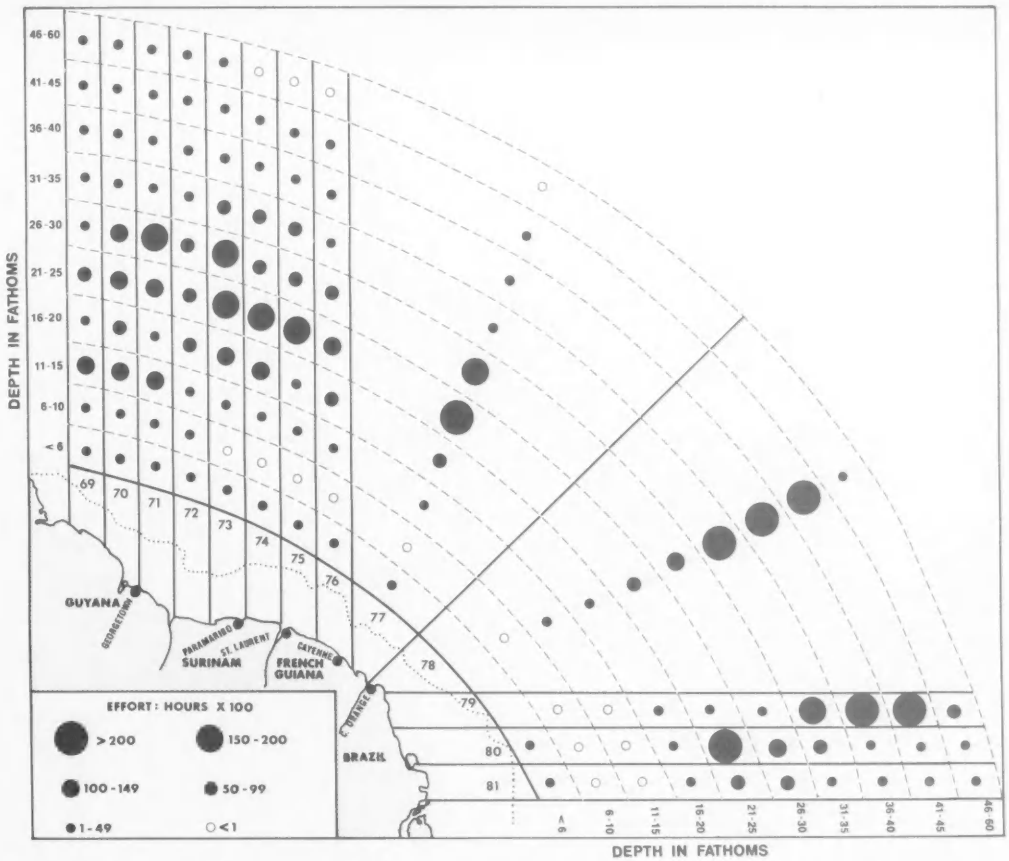

FIGURE 10.—Distribution by fishing zone and water depth of the fishing effort reported on logbooks by U.S. vessels in the Guianas–Brazil fishery, July 1972 to December 1974.

that the maximum sustainable yield was 28.7 million pounds, which could be taken by 692 vessels. This estimate was made from the relationship between the logarithm of the annual catch per vessel and average number of vessels (r = 0.80) for the years 1965–74. A linear surplus yield model applied to the data for the same years suggested that the maximum yield was 27.1 million pounds, which could be taken by 531 vessels (r = 0.82) (Figure 14).

The average number of vessels is the only index of total effort available for the fishery before 1972. The double-rigged Florida-type shrimp trawler has been, almost without exception, the only type vessel used in the fishery. Increases in fishing efficiency probably occurred as the length and horsepower of the vessels increased (Jones and Dragovich 1973), and as the addition of refrigeration equipment permitted longer and farther ranging fishing trips; but these changes were minor in the 1965–74 period.

Before 1965 the increase in average annual catch per vessel paralleled the increase in fleet size (Table 5). The catch per vessel rose sharply between 1961 and 1962; from 1962 to 1965 the increase continued but was less pronounced. Presumably, during these early years of the fishery, the efficiency of the fleet increased as familiarity was gained with the fishing grounds. The earlier data, therefore, were not used in the model. After

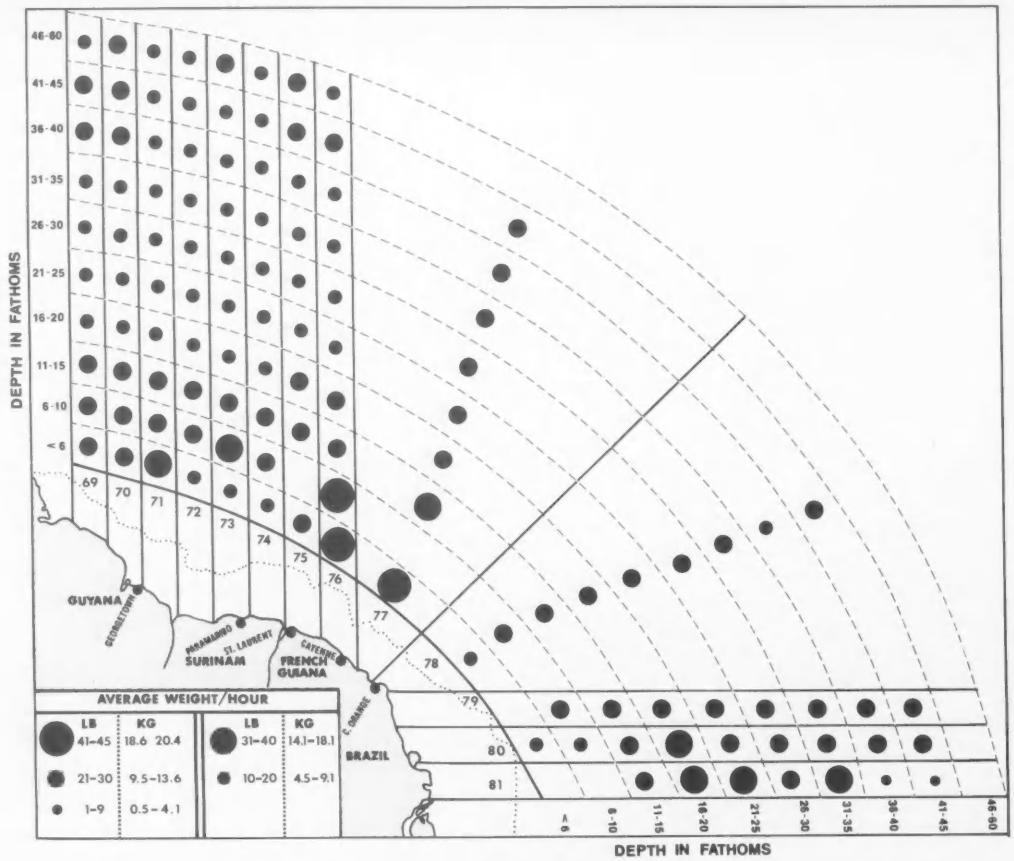

FIGURE 11.—Distribution by fishing zone and depth of the mean catch rate of shrimp for U.S. vessels fishing in the Guianas–Brazil fishery, July 1972 to December 1974. Catch rate is expressed as pounds (and kilograms) of shrimp (heads-off weight) per hour of fishing.

1964, the decline in the average production per vessel was consistent with the increase in the number of vessels. The average annual production per vessel declined from 79,000 lb of shrimp in 1965 to 50,000 lb in 1974; during this time the fleet size increased from 203 vessels (1965) to 460 vessels (1974).

The decline in annual catch per vessel suggests that the average abundance of shrimp available to the fishery has decreased as a result of fishing. Total yields, however, are not depressed at present levels of fishing effort. Apparently the productivity of the resource allows the present level of commercial harvest and also sufficient recruitment to the next generation.

Surplus yield models have been applied in shrimp fishery analysis, though certain assumptions in their use are not completely valid, e.g., instantaneous recruitment, equilibrium conditions, and behavior of the species and populations as a single unit. Also, there is no evidence that the abundance of shrimp recruits is dependent on the abundance of the parent stock in this fishery. Therefore, the prediction of maximum equilibrium yield by a surplus yield model, should be interpreted with caution, especially when the maximum is predicted to occur at fishing effort levels beyond those observed.

The historical shrimp catches follow closely the trends predicted by the surplus yield model (Fig-

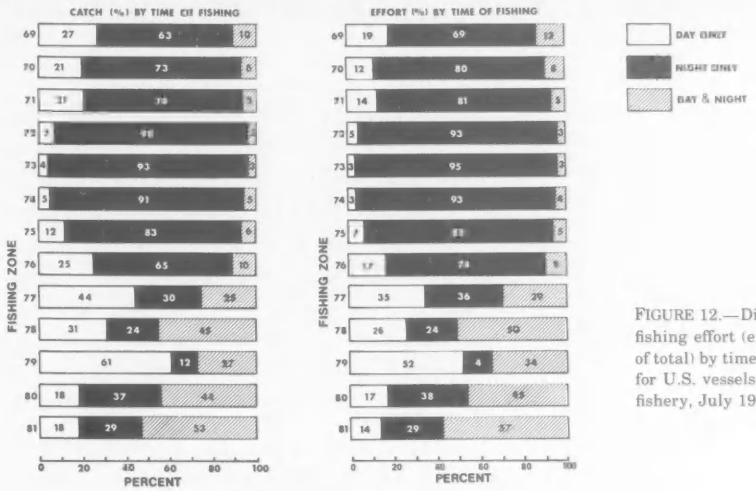

FIGURE 12.—Distribution of catch and fishing effort (expressed as percentage of total) by time of day and fishing zone for U.S. vessels in the Guianas–Brazil fishery, July 1972 to December 1974.

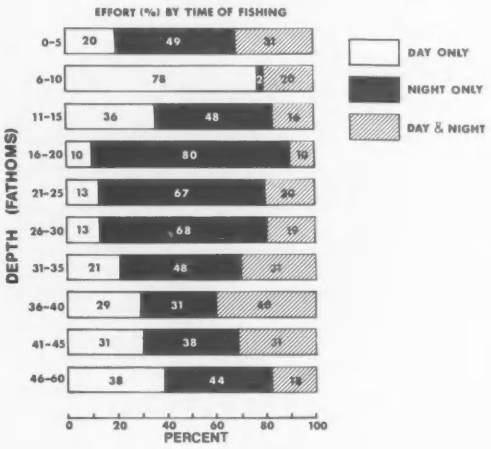

FIGURE 13.—Distribution of fishing effort (expressed as percentage of total) by time of day and water depth for U.S. vessels in the Guianas–Brazil fishery, July 1972 to December 1974.

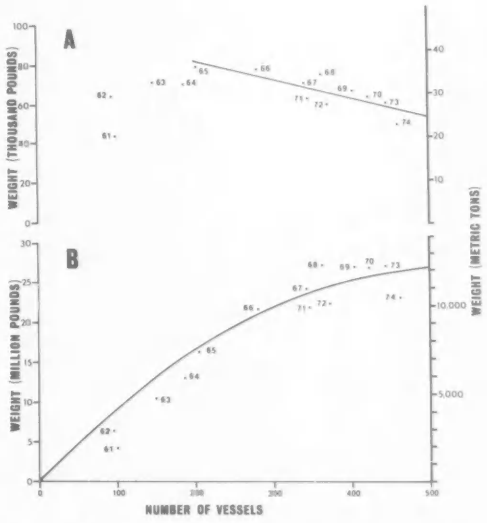

FIGURE 14.—Relationship of the average annual landings per vessel (A) and the total production of shrimp (B) to the total estimated fishing effort (average number of vessels operating) for the Guianas–Brazil shrimp fishery. The linear trend line shown was fitted to the data for the years 1965–74; the estimated production curve was derived from the line in A. The exponential trend line was calculated as explained in the text but is not shown in this figure.

ure 14). From 1961 to 1968 the total production from the fishery rose in proportion to the increase in the number of fishing vessels. In 1969 and 1970 fishing effort increased, but production remained constant at 27 million pounds. Fishing was reduced in 1971 and the catch, therefore, declined. After 1971, catch and effort continued upwards at rates similar to those in the early years of the fishery and a catch of 27 million pounds was again attained in 1973. In 1974 the number of vessels remained high, but the catch declined to 23 million pounds.

The variation of the annual catches from those predicted by the model were 53% and 31% in 1961

TABLE 5.—Average annual catch of shrimp (in pounds, heads-off weight) per vessel by country. Data are derived from Tables 3 and 4.

Year	Barbados	Trinidad	Venezuela	Guyana	Surinam	French Guiana	Brazil	Total
1961	—	—	—	65,700	11,175	—	—	43,890
1962	—	—	—	71,194	44,667	—	—	64,562
1963	—	—	—	67,865	55,480	84,515	—	71,667
1964	49,367	—	—	86,222	68,360	58,059	—	70,241
1965	78,792	—	—	83,833	88,920	68,276	—	79,419
1966	75,000	55,488	—	90,914	86,559	69,672	—	78,089
1967	68,094	58,483	—	79,965	50,720	81,787	—	71,409
1968	73,429	89,167	—	68,366	62,509	87,333	—	75,439
1969	57,472	70,937	—	73,725	68,176	59,791	74,000	67,333
1970	53,560	56,064	—	72,883	64,255	58,639	63,167	64,268
1971	—	55,767	—	60,263	68,511	75,983	64,238	63,523
1972	—	37,855	—	61,389	63,964	75,883	60,000	60,530
1973	77,000	36,048	61,350	60,000	62,683	80,029	62,500	61,673
1974	41,143	46,359	—	55,510	42,047	52,581	50,000	50,222

and 1962, respectively, but for 1963–74 they ranged from 3% to 18%, averaging 8.5%. These variations in catches are deviations about the mean condition predicted by the model. The deviations include the effects of dynamic environmental conditions, but also include random variations and the failure of the model to predict the effects of fishing.

The *Penaeus* shrimp fishery operates mostly on a single year class and year-to-year fluctuations in shrimp populations are to be expected because of the short life cycle of the species. Fluctuations in the annual yield of shrimp are partly the result of variations in spawning success and in survival of young in the inshore nursery grounds, which are generally subject to more extreme variations in environmental conditions than the offshore habitat of adult shrimp. An important management problem for this shrimp fishery is to predict and utilize annual fluctuations in the populations, rather than to only predict an equilibrium yield at a constant level of fishing effort. This will require more detailed knowledge of growth, mortality, and recruitment patterns of the shrimp and the application of yield-per-recruit and stock-recruitment models.

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APPENDIX TABLE 1.—Catches by area and month for the Guianas–Brazil shrimp fishery reported by U.S. vessels. Catches are reported by month in which capture was made; landings are reported by month in which trip was completed.

Item	1972 July	Aug.	Sept.	Oct.	Nov.	Dec.
Catches:						
Zones 69–77:						
No. drags	501	2,433	2,301	2,740	3,269	3,473
No. hours	2,950	12,705	12,815	14,809	18,580	19,666
Catch (pounds[1])	56,530	250,097	230,857	300,346	357,385	361,234
Catch/drag	112.8	102.8	100.3	109.6	109.3	104.0
Catch/hour	19.2	19.7	18.0	20.3	19.2	18.4
Zones 78–81:						
No. drags	909	1,184	1,643	1,537	737	
No. hours	5,234	6,785	9,485	8,477	4,120	
Catch (pounds[1])	125,351	141,194	222,711	184,178	82,260	
Catch/drag	137.9	119.3	135.6	119.8	111.6	
Catch/hour	23.9	20.8	23.5	21.7	20.0	
Total:						
No. drags	1,414	3,617	3,946	4,285	4,006	
No. hours	8,205	19,490	22,310	23,334	22,700	
Catch (pounds[1])	182,311	391,291	454,518	485,894	439,645	
Catch/drag	128.9	108.2	115.2	113.4	109.7	
Catch/hour	22.2	20.1	20.4	20.8	19.4	
Landings (pounds[1])	715,929	940,223	777,443	888,829	747,252	889,776
Percent of landings reported on fishing logs	6.1	34.8	56.5	52.6	57.2	53.1

Item	1973 Jan.	Feb.	Mar.	Apr.	May	June
Catches:						
Zones 69–77:						
No. drags	3,636	3,119	1,308	1,289	1,580	2,216
No. hours	20,522	16,996	6,804	7,154	8,692	12,677
Catch (pounds[1])	437,420	390,142	172,585	181,845	205,385	309,276
Catch/drag	120.3	125.1	131.9	141.1	130.0	139.6
Catch/hour	21.3	23.0	25.4	25.4	23.6	24.4
Zones 78–81:						
No. drags			2,366	3,511	3,024	3,208
No. hours			12,005	18,694	16,888	17,435
Catch (pounds[1])			501,250	692,390	493,075	519,053
Catch/drag			211.8	197.2	163.0	161.8
Catch/hour			41.8	37.0	29.2	29.8
Total:						
No. drags			3,682	4,883	4,629	5,461
No. hours			18,857	26,022	25,726	30,334
Catch (pounds[1])			674,735	882,175	700,950	832,369
Catch/drag			183.2	180.7	151.4	152.4
Catch/hour			35.8	33.9	27.2	27.4
Landings (pounds[1])	774,056	967,677	1,145,173	1,589,147	1,346,502	1,226,817
Percent of landings reported on fishing logs	47.9	53.2	35.2	58.6	56.2	62.1

Item	1973 July	Aug.	Sept.	Oct.	Nov.	Dec.
Catches:						
Zones 69–77:						
No. drags	2,450	2,007	1,675	2,144	2,422	3,249
No. hours	13,772	11,932	9,663	12,023	14,254	18,683
Catch (pounds[1])	329,048	251,585	192,636	249,005	237,945	332,835
Catch/drag	134.3	121.1	115.0	116.1	98.2	102.4
Catch/hour	23.9	21.1	19.9	20.7	16.7	17.8
Zones 78–81:						
No. drags	2,922	2,118	2,362	2,746	948	
No. hours	16,920	11,814	13,323	9,612	5,683	
Catch (pounds[1])	588,729	374,325	367,835	225,950	109,200	
Catch/drag	201.5	176.7	155.7	129.4	115.2	
Catch/hour	34.8	31.7	27.6	23.5	19.2	
Total:						
No. drags	5,409	4,195	4,037	3,903	3,370	
No. hours	30,914	23,746	22,986	21,723	19,937	
Catch (pounds[1])	922,557	625,910	560,471	476,785	347,145	
Catch/drag	170.6	149.2	138.8	122.2	103.0	
Catch/hour	29.8	26.4	24.4	21.9	17.4	
Landings (pounds[1])	1,291,120	1,362,976	1,049,902	1,147,035	824,470	844,284
Percent of landings reported on fishing logs	67.3	55.2	52.9	47.0	46.9	44.9

[1]Heads-off weight.

APPENDIX TABLE 1.—Continued.

Item	1974 Jan.	Feb.	Mar.	Apr.	May	June
Catches:						
Zones 69–77:						
No. drags	4,028	3,425	2,348	2,473	3,103	2,563
No. hours	22,242	19,319	12,167	12,471	15,962	14,816
Catch (pounds[1])	509,163	360,836	266,896	259,317	297,838	246,021
Catch/drag	126.4	105.3	113.7	104.9	96.0	96.0
Catch/hour	22.9	18.7	21.9	20.8	18.6	16.6
Zones 78–81:						
No. drags			3,145	2,845	3,039	2,531
No. hours			17,152	16,011	17,388	13,878
Catch (pounds[1])			417,937	356,270	356,450	312,685
Catch/drag			132.9	125.2	117.3	123.5
Catch/ hour			24.4	22.2	20.5	22.5
Total:						
No. drags			5,551	5,354	6,190	5,163
No. hours			29,649	28,712	33,696	29,203
Catch (pounds[1])			691,463	624,907	664,083	571,941
Catch/drag			124.6	116.7	107.3	110.8
Catch/hour			23.3	21.8	19.7	19.6
Landings (pounds[1])	757,189	772,844	704,377	1,072,920	94,834	832,016
Percent of landings reported on fishing logs	55.1	59.2	79.3	58.0	63.5	83.3

Item	1974 July	Aug.	Sept.	Oct.	Nov.	Dec.
Catches:						
Zones 69–77:						
No. drags	2,183	1,977	2,131	2,813	3,478	3,038
No. hours	13,059	11,599	12,156	16,936	20,658	18,482
Catch (pounds[1])	213,244	159,665	167,545	229,588	282,405	237,991
Catch/drag	97.7	80.8	78.6	81.6	81.2	78.3
Catch/hour	16.3	13.8	13.8	13.6	13.7	12.9
Zones 78–81:						
No. drags	2,975	3,063	1,959	873	91	
No. hours	17,640	18,486	11,724	5,427	577	
Catch (pounds[1])	375,697	334,250	165,865	61,130	6,585	
Catch/drag	120.2	109.1	84.7	70.0	72.4	
Catch/hour	20.3	18.1	14.1	11.3	11.4	
Total:						
No. drags	5,158	5,040	4,090	3,686	3,569	
No. hours	30,699	30,085	23,880	22,363	21,235	
Catch (pounds[1])	571,961	494,915	333,410	290,718	288,990	
Catch/drag	110.9	98.2	81.5	78.9	81.0	
Catch/hour	18.6	16.4	14.0	13.0	13.6	
Landings (pounds[1])	864,569	813,548	548,299	617,972	523,404	520,493
Percent of landings reported on fishing logs	59.9	66.8	66.4	58.4	47.8	62.4

[1]Heads-off weight.

SEASONAL CYCLE OF ZOOPLANKTON ABUNDANCE AND SPECIES COMPOSITION ALONG THE CENTRAL OREGON COAST

WILLIAM T. PETERSON AND CHARLES B. MILLER[1]

ABSTRACT

Species composition of zooplankton collected during 3 yr of sampling close to the coast at Newport, Oreg., varied with season. In all seasons the most abundant plankters were copepods. Dominant species in summer were *Pseudocalanus* sp., *Acartia clausii*, *A. longiremis*, *Calanus marshallae*, and *Oithona similis*. These are primarily coastal forms with northern affinities, and they were present all year. Dominant species in winter were *Paracalanus parvus* and *Ctenocalanus vanus*, forms of southern affinities. They tended to disappear completely in summer. These geographic affinities are in correspondence with the source regions for surface waters that are implied by the direction of flow in the different seasons. Abundances are about one order of magnitude higher in summer than in winter. Copepod diversity is greater in winter than summer: the winter checklist contains 51 species, while the summer list contains only 38 species.

An analysis of differences in the zooplankton of the three winter periods of the study shows 1969–70 to have had much greater dominance by southern forms and a larger variety of them than 1970–71 or 1971–72. This corresponds with differences in the wind patterns between the years. Winds in the winter of 1969–70 were gentle and directly from the south, while the other winters had the more usual southwesterly storms. Gentle winds directly from the south were more effective at moving surface water northward alongshore than southwesterly storms, despite their lesser overall northerly component.

The hydrography and pelagic ecology of the Pacific Ocean very close to the Oregon coast are strongly seasonal. Winter winds from the southwest, which produce surface flow from the south and toward shore, alternate with summer winds from the north, which produce flow from the north and away from shore, generating coastal upwelling. These seasonal changes in the source of currents flowing through the area cause changes in the species of zooplankton that are present. In this paper we describe this cycle of change in species composition from a series of samples collected along a transect normal to the coast at Newport, Oreg., approximately every 2 wk from June 1969 through July 1972. In a previous paper (Peterson and Miller 1975) we have used these data to make a detailed comparison of the upwelling seasons of the years 1969, 1970, and 1971 with emphasis upon the differences between years. Here we consider the entire annual cycle with emphasis upon consistent aspects of the differences between seasons. The discussion includes a consideration of the differences between the three winters of the study.

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MATERIALS AND METHODS

Detailed description of collection and laboratory procedures are given in Peterson and Miller (1975, 1976). Plankton samples were collected with a 240-μm mesh net hauled obliquely from near the bottom to the surface at stations 2, 5, 9, and 18 km from the Oregon coast along a transect at lat. 44°40′N. The stations will be referred to as NH 1, NH 3, NH 5, and NH 10, respectively, which stand for Newport Hydrographic stations at 1, 3, 5, and 10 n.mi. from the shore. Water depths for the four stations were 20, 46, 55, and 80 m. Surface temperature and salinity measurements were made at most stations, and a bathythermograph was usually lowered. A total of 213 samples from 56 dates are included in the present analyses. Distribution of samples among stations, exact dates, and complete data for all samples can be found in Peterson and Miller (1976).

There are important limitations on the zooplankton data. We chose to express numerical abundance as numbers of individuals per cubic meter (no. m^{-3}). Because our nets were towed obliquely through the entire water column, the quantitative abundance estimates are actually abundances averaged over the water column. If an

animal is equally abundant at all depths, then oblique tows will adequately estimate its abundance. If an animal is restricted to a narrow surface layer, then its abundance will be underestimated by deeper tows relative to shallower ones. Recent work by ourselves and Myers (1975) has shown that highest zooplankton abundances are found within the top 20 to 30 m of the water column. Therefore, our oblique tows from depths greater than about 30 m do underestimate zooplankton abundances. This becomes a problem for tows taken at stations farther from shore as the water depth increases, because an increasing fraction of the water column sampled contains few animals. Therefore, abundance gradients should not be considered to be real between stations NH 1 (water depth = 20 m) and NH 10 (water depth = 80 m) unless abundance differences are greater than a factor of four.

Abundances are also underestimated for many copepod taxa because the small copepodite stages could easily pass through our 240-μm mesh net. Copepodites of species of *Pseudocalanus* and *Acartia* younger than stage III were seldom seen in our samples. Probably only stages IV and V were sampled quantitatively.

The data set gains its value from being a 3-yr time series of samples collected in exactly the same manner at the same stations. As such, these are good baseline data to which future work can be compared. Point estimates of abundance have little meaning, but comparisons of abundances between seasons and years at a set of stations are valid and meaningful.

TABLE 1.—A checklist of copepod species taken off Newport, Oreg., in summer (S) and winter (W) months during the period of the study.

[C = Common, occurrence in >50% of the samples taken, U = Unusual, occurrence in <50% but >5 samples taken, R = Rare occurrence <5 samples.]

Copepod species	S	W	Copepod species	S	W
Calanus marshallae	C	C	*Metridia lucens*[2]	C	C
C. tenuicornis	U	C	*M. pacifica*[2]	U	
C. plumchrus	R	U	*Lucicutia flavicornis*	U	U
C. cristatus		R	*Candacia columbiae*		R
Rhincalanus nasutus	R	R	*C. bipinnata*	R	R
Eucalanus bungii	U	U	Immature *Heterorhabdus*		
Mecynocera clausii		U	spp.		R
Paracalanus parvus	C	C	*Pleuromamma borealis*		R
Calocalanus styliremis		U	*P. abdominalis*		R
C. tenuis		U	*Centropages abdominalis*	C	U
C. sp.		R	*Epilabidocera amphitrites*	U	U
Pseudocalanus sp.[1]	C	C	*Acartia clausii*	C	C
Microcalanus pusillus	U	U	*A. longiremis*	C	C
Clausocalanus masti-			*A. tonsa*	U	C
gophorus		U	*A. danae*		R
C. furcatus		R	*Eurytemora americana*	R	
C. arcuicornis	U	C	*Tortanus discaudatus*	U	U
C. jobei		R	*Microsetella* sp.	U	U
C. pergens	U	C	*Sapphirina* sp.	U	U
C. parapergens		U	*Oithona similis*	C	C
C. paululus		R	*O. spinirostris*	C	C
Ctenocalanus vanus	U	C	*Oncaea tenella*	R	R
Aetideus pacificus	U		*O. borealis*	R	R
Immature *Gaidius* spp.	U		*O. conifera*	R	R
Gaidius brevispinus		R	*O. mediterranea*	R	R
Immature *Gaetanus* spp.	R		*O. dentipes*		R
Gaetanus simplex		R	*O. subtilis*		R
Paraeuchaeta japonica	R	R	*O. media hymena*	R	
Racovitzanus antarcticas	U		*Corycaeus anglicus*	R	C
Scolecithricella minor	U	U	*C. amazonicus*		R

[1]Pacific representatives of the genus *Pseudocalanus* are not adequately described. They are being studied by B. Frost.

[2]Two morphs of the genus *Metridia* were separated on the basis of the shape of the prosome in lateral view. The *M. pacifica* type is more robust and has a steeply sloping forehead. Detailed morphological analysis of the two types has not been done.

RESULTS

Frequency of Occurrence of Zooplankton Taxa

Copepods were the most frequently occurring and the most abundant members of the zooplankton community in the nearshore region off Newport, Oreg. Fifty-eight species were seen in our samples (Table 1). Thirty-eight species were found in the summer samples and 51 species in the winter samples. During our study, species from the Subarctic, Transition, and Central Pacific faunal groups (McGowan 1971) were taken.

The copepods in Table 1 can be grouped on the basis of patterns of occurrence. Eight species occur commonly during both winter and summer months: *Calanus marshallae, Paracalanus parvus, Psuedocalanus* sp., *Metridia lucens, Acartia clausii, A. longiremis, Oithona similis,* and *O. spinirostris.* Seven species were found only during the summer months and probably have northern affinities: *Aetideus pacificus, Gaidius* immatures, *Gaetanus* immatures, *Racovitzanus antarcticas* s.l., *Metridia pacifica,* and *Oncaea media hymena. Eurytemora americana* occurred very rarely in the sample series, but it is a common form in all of the local estuaries (Frolander et al. 1973). Only one species was common during the summer and uncommon during the winter: *Centropages abdominalis.* This species has northern affinities. A group of six species had the opposite characteristic; that is, they were common during the winter but uncommon or rare during the summer: *Calanus tenuicornis, Clausocalanus arcuicornis, C. pergens, Ctenocalanus vanus* s.l., *Acartia tonsa,* and *Corycaeus anglicus.* All of these species are common in warmer water south of Oregon.

The majority of the copepod species (43) were

always uncommon or rare in our samples and probably have unimportant roles in the community. However, taxonomic study of these rare or uncommon species is important because in many cases their presence indicates the presence of a particular water type or mixture of types. Most of the species that are found off Newport only during winter months have southern affinities (Central Pacific waters). They are transported north along the continental shelf by the Davidson Current and are probably very near the extreme northerly limit of their range. These species were *Mecynocera clausii*, *Calocalanus styliremis*, *C. tenuis*, *Calocalanus* sp., *Clausocalanus mastigophorus*, *C. furcatus*, *C. jobei*, *C. parapergens*, *C. paululus*, *Acartia danae*, *Corycaeus amazonicus*, *Oncaea dentipes*, and *O. subtilis*. Other species that were found only during winter months have northern affinities and are usually found in deep water over the continental slope. They were probably transported shoreward as a result of onshore winds. These species were *Calanus cristatus*, *Gaidius brevispinus*, *Gaetanus simplex*, *Candacia columbiae*, *Heterorhabdus* immatures, *Pleuromamma borealis*, and *P. abdominalis*. The 16 species that were rare or uncommon in both summer and winter include representatives of both northern and Central Pacific faunal groups.

Seasonal Cycle of Total Zooplankton Abundance

The annual cycles of total zooplankton abundance for stations NH 1, NH 3, NH 5, and NH 10 are shown in Figures 1, 2, and 3. Abundance is high during the upwelling season and often remains high during the autumn period of hydrographic transition. Abundance is low during the period from November through April. All four stations have this basic pattern, but there are important changes with distance offshore. Table 2 gives several indices of cycle amplitude. The amplitude of the cycle is greater inshore. First, there are more dates at NH 1 and NH 3 with densities in excess of 5,000 m^{-3} (an arbitrary value). Second, the absolute difference between summer and winter density decreases with distance from shore. All of the decrease in the ratio of the densities in the two seasons occurs between 2 and 5 km from shore (NH 1 to NH 3).

There is a suggestion in the data for NH 1 (Figure 1) that the annual cycle of zooplankton abundance is more complex than just a summer high

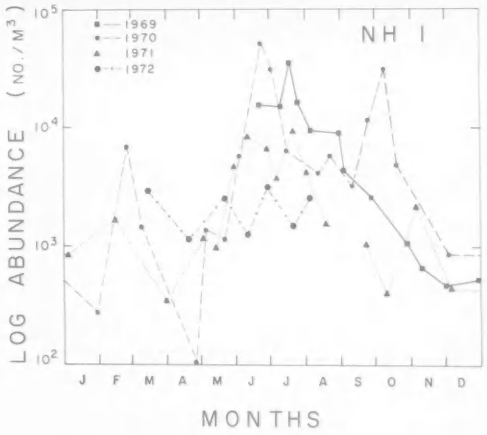

FIGURE 1.—Annual cycle of totaled zooplankton abundance 2 km from the Oregon coast at Newport (NH 1) during the 3-yr study period.

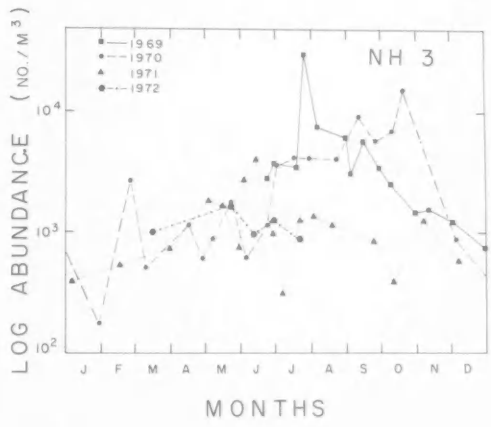

FIGURE 2.—Annual cycle of totaled zooplankton abundance 5 km from the Oregon coast at Newport (NH 3) during the 3-yr study period.

TABLE 2.—Some indices of the amplitude of the seasonal cycle of zooplankton density off the Oregon coast. Median density estimates for summer and winter seasons at the four stations on the Newport, Oreg., transect, the ratio of median densities between seasons, and the number of dates with densities >5,000 m^{-3}.

Station	Summer (May–Oct.)	Winter (Nov.–Apr.)	Summer–winter ratio	No. dates with density >5,000 m^{-3}
NH 1	4,350 m^{-3}	850 m^{-3}	5.1	17
NH 3	2,250 m^{-3}	800 m^{-3}	2.8	8
NH 5	1,550 m^{-3}	530 m^{-3}	2.9	4
NH 10	1,000 m^{-3}	365 m^{-3}	2.7	0

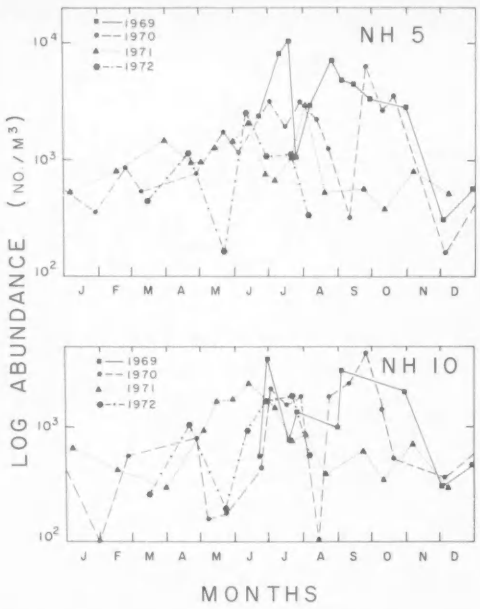

FIGURE 3.—Annual cycle of totaled zooplankton abundance 9 and 18 km from the Oregon coast at Newport (NH 5 and NH 10) during the 3-yr study period.

and a winter low. In addition to that basic cycle, there are peaks in total abundance at NH 1 in each year of the study in either February or March. The 25 February 1970 sample had high numbers of copepod nauplii other than *Calanus* (1,840 m^{-3} = 27% of the total zooplankton). This indicates the presence of an actively reproducing adult copepod population. A diatom bloom was in progress at that time as well. Our nets were clogged with the diatom *Thalassiosira*. The 16 February 1971 peak had high numbers of *Pseudocalanus* sp. (680 m^{-3} = 41% of the catch), *Calanus marshallae* (240 m^{-3} = 15%), and *Calanus* nauplii (192 m^{-3} = 12%). The *Pseudocalanus* sp. population was almost entirely stage I copepodites. These facts again indicate actively reproducing adult copepod populations in late winter. In both of these years, abundances decreased after the February peak to lower values in March or April. In 1972 no samples were collected in January or February. The 15 March sample at NH 1 had high numbers of *Pseudocalanus* sp. (1,844 m^{-3} = 62%), *Oithona similis* (690 m^{-3} = 23%), and *Acartia longiremis* (265 m^{-3} = 9%). Half of the total catch were immature *Pseudocalanus* sp. and half of the *A. longiremis* were immature. Again, there is some evidence of a late winter cycle of reproduction of the species of copepods permanently resident in the nearshore zone and dominant later in the year. There is evidence of this late winter peak in copepod abundance at NH 3 only in 1970, and it is not seen at all in the data for NH 5 and NH 10.

The months of April and May are periods of transition in the direction of the prevailing wind. An atmospheric high pressure cell begins to form over the North Pacific Ocean, and the winds begin to blow from the north with greater frequency. In all years of this study, heavy phytoplankton blooms were observed at NH 1 during this period. The blooms are probably associated with the replenishment of nutrients within the photic zone by the earliest brief episodes of upwelling. Dates with dense blooms were 27 April 1970, 3 and 14 May 1971, 20 April 1972, and 22 May 1972. Zooplankton abundances were low at these times.

Seasonal Cycle of Relative Species Abundance

The seasonal cycle of relative abundance of the most abundant species of copepods is shown in Figure 4 for all four stations. The graphs for each station represent cumulative percentage of the total catch for the species as labelled. The result is complex but deserves careful study because some interesting patterns are present. The simplest pattern is the sinusoidal annual cycle. This pattern is in phase with the seasonal cycle of total abundance. It can be concluded from comparison of the zooplankton abundance plots (Figures 1, 2, 3) and from the relative species abundance plot (Figure 4), that low numbers during winter months are coincident with 1) a decrease in relative abundance of the endemic copepod species and 2) an increase in importance of warmwater species and noncopepod taxa. In addition to copepods with southern affinities, *Oikopleura* spp. and chaetognaths become important during the winter.

There is marked seasonality in the relative abundance of each taxon. This will be discussed station-by-station. At NH 1 *Pseudocalanus* sp. were numerically important during the upwelling season, usually through August. *Acartia clausii* and *A. longiremis* were always important during the autumn after the cessation of upwelling. *Centropages abdominalis* was never a major component after August, with the exception of 1971. *Calanus marshallae* copepodites and nauplii were

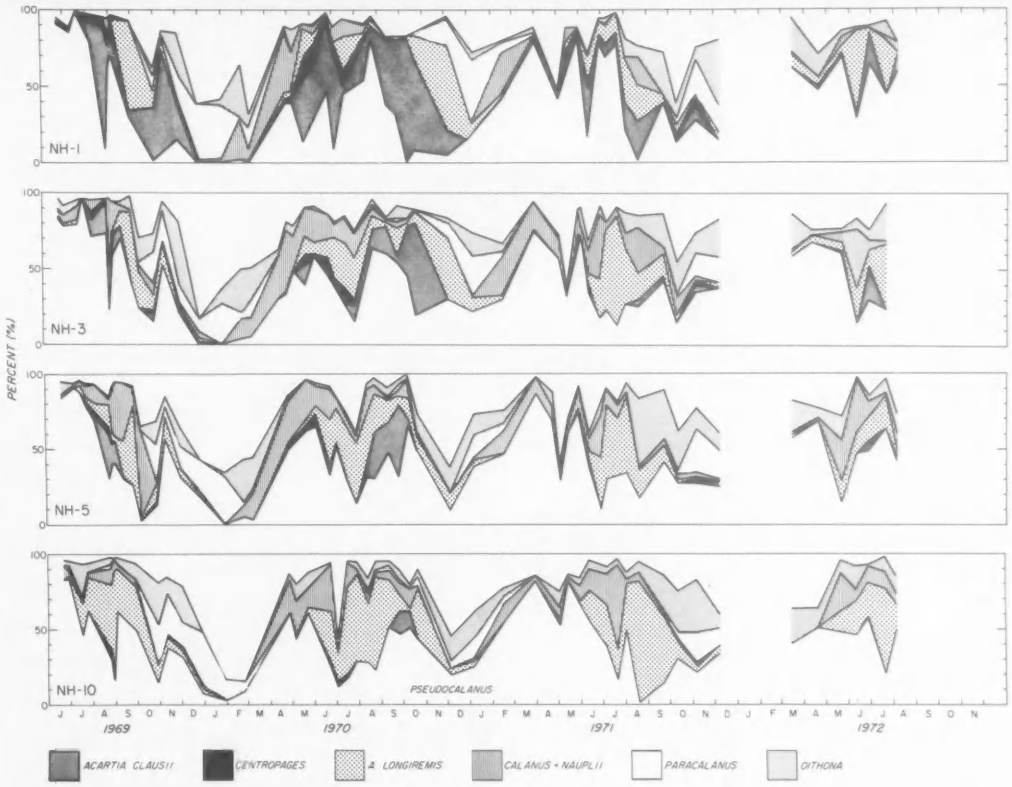

FIGURE 4.—Seasonal cycle of relative abundance (percent of total catch) of the most abundant zooplankton species (all copepods) at stations NH 1, NH 3, NH 5, and NH 10 along the Newport, Oreg., transect over the 3-yr study period. *Centropages* were *C. abdominalis*, *A. longiremis* were *Acartia longiremis*, *Calanus* were *C. marshallae*, *Paracalanus* were *P. parvus*, and *Oithona* were *O. similis*. *Pseudocalanus* sp. are represented by the white area at the bottom of each graph. All remaining zooplankton are represented by the white area at the top of each graph.

most dominant during the spring. *Paracalanus parvus* and *Oithona similis* have their highest relative abundance during the winter.

Different years were different at NH 1, as previously noted (Peterson and Miller 1975). *Pseudocalanus* sp. had a much higher relative abundance during the 1969 and 1971 upwelling seasons than in 1970. During the 1970 upwelling season, *A. clausii* and *Pseudocalanus* sp. shared numerical dominance in many samples. *Centropages abdominalis* was less important during the 1971 upwelling period than in earlier years. *Acartia longiremis* was about equally dominant at various times during all three upwelling seasons. *Oithona similis* was more important during the summers of 1969 and 1971. *Paracalanus parvus* was a significant fraction of the plankton over broader time intervals in 1969 and 1970 than in 1971.

At NH 3 the most striking aspect of the annual cycle compared with NH 1 is the greatly decreased importance of *Acartia clausii* and generally increased importance of *A. longiremis* and *Calanus marshallae*. *Acartia clausii* made up a large fraction of the catch only during October 1970. *Acartia longiremis* and *C. marshallae* were major components over broader intervals in 1970 and 1971 at NH 3 than at NH 1. The annual cycle of *Pseudocalanus* sp. relative abundance at NH 3 was about the same as for NH 1, except for two periods: July of 1970 and 1971. During both times *Pseudocalanus* sp. was dominant at NH 1, whereas *A. longiremis* was dominant at NH 3.

The NH 5 plot is similar to that for NH 3, par-

ticularly between November 1969 and May 1970 and between January and July 1971. Similarly to NH 3, the importance of *A. clausii* is greatly reduced and the importance of *A. longiremis* and *C. marshallae* are increased relative to NH 1. The NH 10 plot follows the NH 5 plot closely during 1970 and 1971 with one exception: in September 1970 *A. clausii* was a significant component at NH 5 but not at NH 10.

DISCUSSION

The annual cycle in the species composition of the zooplankton community along the Oregon coast must result from the annual cycle of the nearshore circulation, which is well described by Huyer et al. (1975). There is an exact correspondence between the sources of currents implied by the direction of flow in each season and the geographic affinities of the species occurring in the water. In summer, when the net water transport is to the south, species with northern affinities dominate. In winter, when transport is northward, species with southern affinities are mixed with the indigenous fauna. Abundances are about an order of magnitude higher in summer than winter, presumably because of production stimulated by coastal upwelling. We term the summer dominants "indigenous" both because they are present throughout the year and because they are the forms which reproduce and complete their life cycles in the Oregon nearshore zone. None of these forms is endemic, however, in that the distributions of all of them extend north around the rim of the Gulf of Alaska and into the Bering Sea. New studies now in progress are intended to describe the distributions within the upwelling ecosystem of the life cycle stages of the summer dominants, and to explain the maintenance of their populations within the system of nearshore currents.

A similar interpretation of seasonal changes in zooplankton species present off Oregon was offered by Cross and Small (1967). They used *Acartia danae* as an indicator of transport from the south (following Frolander 1962), and *Centropages abdominalis* (called *C. mcmurrichi* in their paper) as an indicator of flow from the north. In the present study *A. danae* was very infrequent, and a variety of other species (*Paracalanus parvus, Ctenocalanus vanus, Clausocalanus pergens,* etc.) appear to be much better indicators of southern sources. The studies were different in that the earlier one sampled farther offshore, and it began with the notion that *A. danae* would be an indicator, rather than examining the fauna as a whole.

While there is a generally similar sequence each year in the changes of the copepod species and their abundance, there are also marked differences in these changes between years. These were discussed for the upwelling season by Peterson and Miller (1975). We would like to add to that a brief evaluation of some differences between the winters of our study. Temperature–salinity diagrams including all of the data collected at our inshore stations during the months of October through March are shown in Figure 5. The winter of 1969–70 was warmer than the other winters. Progressive vector diagrams of the winds in each of the winter periods of our study are shown in Figure 6. The winds during 1969–70 were different from those of 1970–71 and 1971–72. During the fall and winter months of 1969–70 there were

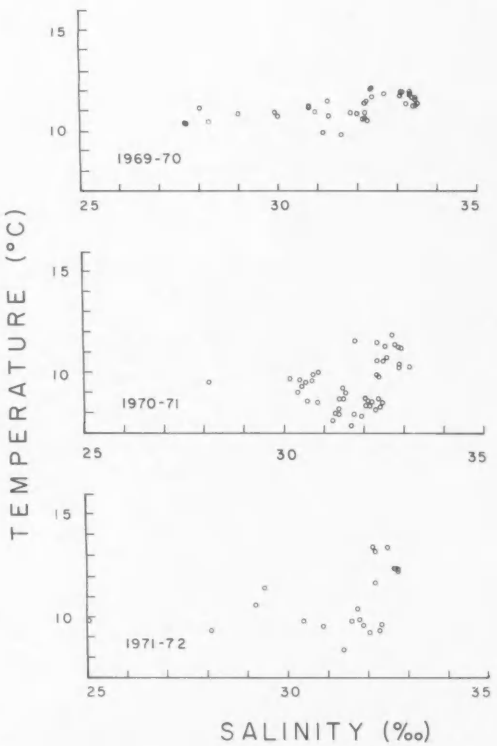

FIGURE 5.—Temperature–salinity scatter diagrams combining data from stations NH 1, NH 3, NH 5, and NH 10 along the Newport, Oreg., transect for the winters of 1969–70, 1970–71, and 1971–72 from October through March.

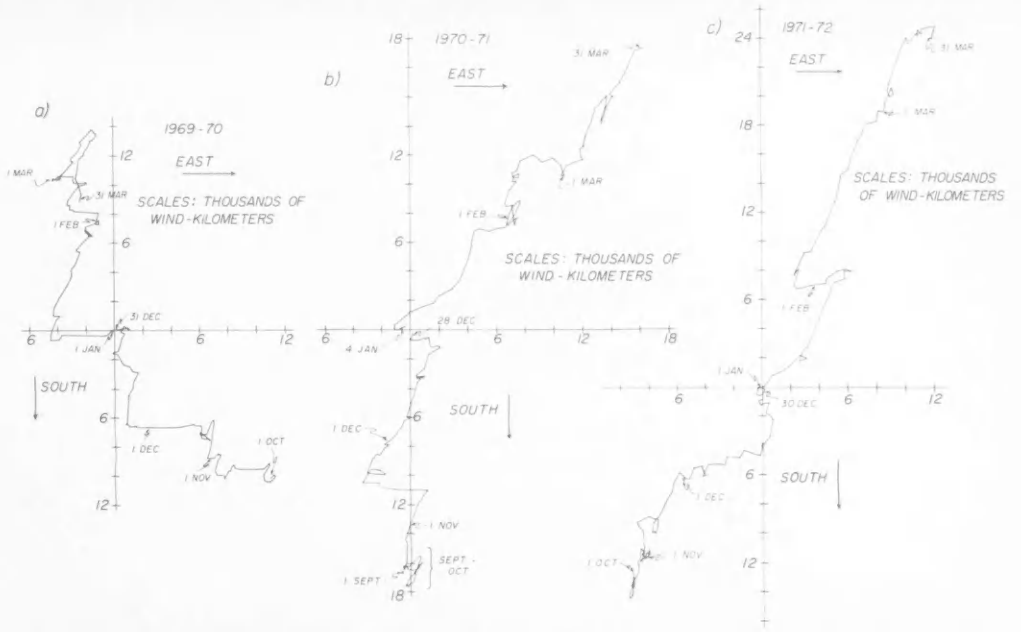

FIGURE 6.—Progressive vector diagrams for the wind at Newport, Oreg., for the winters of 1969–70, 1970–71, and 1971–72.

three intervals with winds from the east: most of October, 23 November to 8 December, and 30 December to 12 January. The entire 6-mo period of winter winds lacked the southwesterly storms that are characteristic of most winters. The other two winter wind patterns shown in Figure 6 are more typical on the basis of comparisons to the winters of later years (1972–73, 1973–74, 1974–75).

Upwelling index data taken from Bakun (1973) for the winters of our study are presented in Table 3. Negative values of the index indicate winds that will produce shoreward convergence of surface waters on the average over the month. Negative values of the anomaly indicate greater-than-usual shoreward convergence. Indices for winter 1969–70 are quite different from those of the other two winters. Onshore convergence was anomalously high in 1969–70 and anomalously low in 1970–71 and 1971–72.

The zooplankton data (see Peterson and Miller (1976) for detailed tabulations) indicate that the northward flow of the Davidson Current probably was much greater in 1969–70 than in the other two years. A number of southern zooplankton species had their greatest abundance during that winter: *Clausocalanus jobei, C. paululus, Oncaea dentipes,* and *O. subtilis*. All of the above 16 copepod species are indicators of water originating south of at least Cape Mendocino, Calif. (Olsen 1949; Fleminger 1964, 1967; Frost and Fleminger 1968).

TABLE 3.—Monthly upwelling index values from Bakun (1973) for midwinter period at lat. 45°N, just north of the Newport, Oreg., transect, during the years of our study.

Month	20-yr mean index for month	1969–70		1970–71		1971–72	
		Index	Anomaly	Index	Anomaly	Index	Anomaly
Nov.	−74	−53	+21	−54	+19	−40	+34
Dec.	−93	−157	−64	−106	−12	−27	+66
Jan.	−94	−98	−4	−32	+62	−19	+75
Feb.	−47	−71	−24	−16	+32	−103	−56
Total			−71		+101		+119

The physical implication of this set of biological observations is that winter periods of gentle winds directly from the south (Figure 6a) are much more effective at moving water northward alongshore than winter periods of violent southwesterly storms (Figures 6b, c), even though the total northward component of the winds during the stormy winters might be much greater. This is in agreement with the temperature results (Figure 5) and with the anomaly in the upwelling indices.

Bakun (1973) pointed out that winters of extreme shoreward convergence of wind-drifted surface waters (negative index anomaly) should cause the density structure to be depressed toward the coast and should accelerate northward flow or decelerate southward flow. "Either situation would favor an anomalous warm advection," according to Bakun.

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GROWTH AND REPRODUCTION OF THE EASTERN SPINNER DOLPHIN, A GEOGRAPHICAL FORM OF *STENELLA LONGIROSTRIS* IN THE EASTERN TROPICAL PACIFIC

WILLIAM F. PERRIN, DAVID B. HOLTS, AND RUTH B. MILLER[1]

ABSTRACT

Estimates of life history parameters for use in assessing status of the population of the eastern spinner dolphin and assessing impact of incidental mortality in the yellowfin tuna fishery are developed from data on 2,675 specimens collected from 1968 to 1975. Average length at birth is 77.0 cm, gestation is 10.6 mo, average length at 1 yr is approximately 134 cm. Three alternative hypotheses of rate of deposition of dentinal growth layers are: I) 1.5 layers/yr throughout life; II) 1.5 layers in the first year, 1/yr thereafter (most favored hypothesis); and III) 1.5 layers until puberty (at 5.5 layers in females and 9 layers in males), and 1/yr thereafter. Males attain sexual maturity on the average at about 170 cm (range 160–195) and 9–12 layers (6.0–11.5 yr), depending on the criterion of testis–epididymis weight chosen. Average length at attainment of social maturity is unknown. Average length of adult males is 174–176 cm. Females on the average attain sexual maturity at 165 cm (5.5 layers or 3.7, 5.0, or 3.7 yr under Hypotheses I, II, and III). Average length of sexually adult females is 171 cm (range 152–187). Ovulation rate is 1/growth layer (1/0.67–1.00 yr) until about 10 ovarian corpora have been accumulated, after which the rate declines. Approximately 1% of adult females are postreproductive. Best estimates of annual pregnancy rate range from 0.450 (based on 1973 data) to 0.474 (based on 1974 data). The pooled estimate for all years' data is 0.461. The corresponding estimates of calving interval (reciprocal of pregnancy rate) are 2.22 yr, 2.11 yr, and 2.17 yr, respectively. Pregnancy rate decreases after age of about 12 layers (8.0, 11.5, or 10.2 yr) concomitant with increase in lactation rate. Overall sex ratio is near parity, but there are about 6% more females than males in adults. Best estimates of gross annual reproductive rate based on the 1973, 1974, and 1975 data are 0.099, 0.103, and 0.105, respectively. The estimate based on pooled data for the 3 yr is 0.102. The estimates are compared with estimates for the spotted dolphin, *Stenella attenuata*, and for other cetaceans.

This paper presents the results of a study of the life history of the eastern spinner dolphin, a geographical form[2] of *Stenella longirostris* (Gray 1828), in the eastern tropical Pacific. The eastern spinner dolphin accounted for the second-highest level of incidental mortality in the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific through 1975, after the offshore spotted dolphin, a form of *S. attenuata* (Gray 1846) (Perrin 1969, 1975a; Perrin et al.[3]) The purpose of the study was to develop estimates of life history parameters for use in assessing the status of the eastern spinner dolphin stock and the impact on the stock of incidental mortality in the yellowfin tuna fishery. Preliminary results of partially completed analyses reported here in full appeared in Perrin et al.[4]

Very little previously published information is available on growth and reproduction of the pantropically distributed *S. longirostris*. Cadenat and Doutre (1959) listed body weights and gonadal

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[2]Perrin (1975b) gave the eastern spinner dolphin subspecific rank but stated that the nomenclature is not yet resolved, because the holotype of the species is from an unknown locality. The term "geographical form" is used here as a substitute for the more unwieldy "[*Stenella longirostris*] subspecies (unnamed)." The term "dolphin" is used in conformance with the "list of smaller cetaceans recognized" adopted by the Subcommittee on Smaller Cetaceans, Scientific Committee, International Whaling Commission (Anonymous 1975).

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FISHERY BULLETIN: VOL. 75, NO. 4, 1977.

data for two males (1,940 and 2,040 mm) and two females (1,790 and 1,800 mm) from off Senegal in the tropical Atlantic. Layne (1965) published similar data for two males (1,845 and 1,910 mm) and one female (1,965 mm) from Florida. Pilson and Waller (1970) reported on an adult female of *S. microps* [= *S. longirostris*] 176 cm long, from the eastern Pacific. Harrison et al. (1972) published detailed length, weight, and gonadal data for 12 males (79 to 185 cm) and 21 females (86 to 188 cm) of *S. longirostris* from the eastern Pacific; five males (150 to 182 cm) and two females (169 and 179 cm) of *S. roseiventris* [= *S. longirostis*] from Hawaii; and nine specimens from the eastern Pacific, eight males (165 to 178 cm), and one female (171.5 cm) listed as "probably *S. longirostris*." In their discussion of growth and reproduction, however, they did not differentiate between *S. longirostris* and *S. graffmani* [= *S. attenuata*], a larger species that differs significantly from *S. longirostris* in several features of life history (compare results below with those for *S. attenuata* in Perrin et al. (1976) and Kasuya et al. (1974)).

Several recent reports emanating from the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, have dealt with the developmental components of various aspects of the life history of *S. longirostris* other than reproduction. Perrin (1972) described the development of the color pattern in eastern Pacific forms of the species. Perrin and Roberts (1972) analyzed changes in organ weights with size, based on 14 specimens. Dailey and Perrin (1973) described differences in parasite frequencies correlated with age in 19 specimens. Perrin (1975a, b) described developmental variation in morphology in the eastern Pacific and defined three geographical forms (subspecies), of differing adult size: the less-than-2-m-long "eastern spinner," the subject of this report; the slightly larger "whitebelly spinner," found farther offshore; and the "Costa Rican spinner," which is restricted to the coastal waters of Central America and attains a total length of well over 2 m.

This paper treats only the eastern spinner, the form of *S. longirostris* most heavily involved in the tuna fishery through 1975 in terms of numbers of seine net sets and numbers killed (Perrin 1975a). Some data for the whitebelly spinner are included in certain of the analyses of the eastern spinner, including those of length at birth and of brain weight relative to body length, for reasons explained below. A preliminary report on the whitebelly form of *S. longirostris* appeared in Perrin et al.[5]

METHODS AND MATERIALS

The Field Program

Nearly all of the data were collected by NMFS scientific observers aboard commercial tuna vessels. The data collection procedures were the same as previously described for the spotted dolphin (Perrin et al. 1976). Data on *S. longirostris* were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, and 30 in 1975. Some specimens were also collected in 1970 by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

The Sample

In 1971 and early 1972, when the observer program was very limited, adult female specimens were selected for dissection when available, and the samples for those periods are, therefore, biased with regard to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was practiced in determining which animals were to be examined, and those samples are assumed to be cross-sectional with respect to the kill. Fetuses were not collected in 1968.

The sample of animals for which life history data including at least, but not restricted to, sex and body length includes 2,675 specimens, 2,663 from precisely known localities (Figure 1) and 12 from imprecisely known localities, from the eastern tropical Pacific between lat. 21°N and 3°S and west to long. 117°W. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1). Length-frequency distributions by 5-cm increments for males and females, including fetuses, are presented by year and month in Figures 2 and 3.

[5]Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Preliminary estimates of some parameters of growth and reproduction of the whitebelly spinner dolphin, a geographical form of *Stenella longirostris*, in the eastern tropical Pacific. Working document submitted to Meeting of Subcommittee on Small Cetaceans, Scientific Committee, International Whaling Commission, London, 7–8 June 1976. SWFC Admin. Rep. LJ-76-12, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 36 p. (Unpubl. rep.)

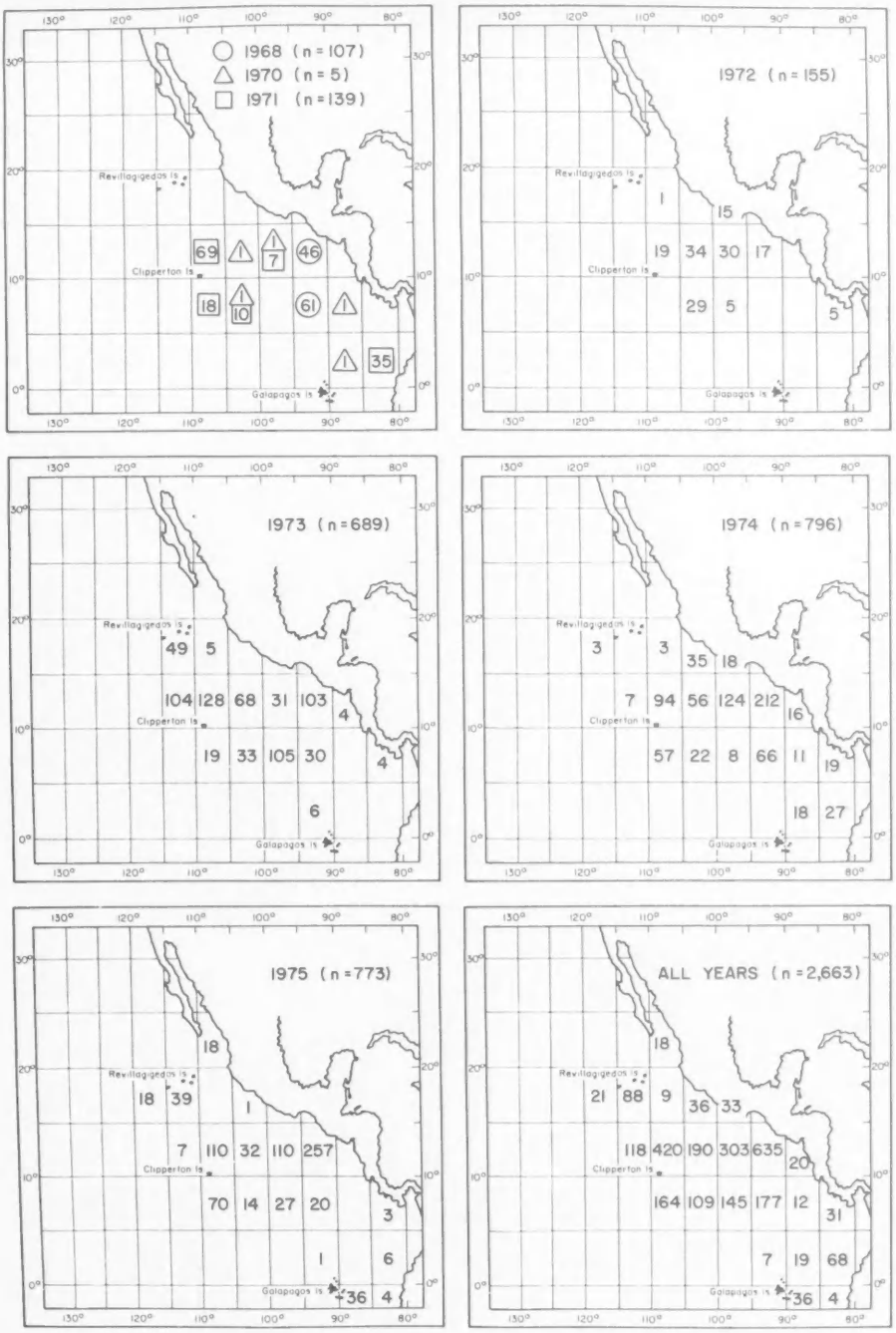

FIGURE 1.—Samples of *Stenella longirostris* collected 1968-75, by 5° square.

TABLE 1.—The sample of eastern spinner dolphins used in the life history analysis, by year and month.

	1968		1970		1971[1]		1972[1]		1973		1974		1975		All years		
Month[2]	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Total
Jan.			1	2	2	11	9	12	23	24	85	104	163	170	283	323	606
Feb.					20	15		15	135	128	230	209	68	72	453	439	892
Mar.							11	35	79	78	26	18	32	31	148	162	310
Apr.	52	55					25	15	50	53	41	30	9	25	177	178	355
May							6	12	1	7	1	3	16	13	24	35	59
June												3	19	21	19	24	43
July			2										16	25	18	25	43
Aug.											3	1	12	12	15	13	28
Oct.							10	7	7	7			17	33	34	47	81
Nov.					35	39			49	45	19	27	12	9	115	120	235
Dec.					6	11			3	3					9	14	23
Total	52	55	3	2	63	76	61	96	347	345	405	395	364	411	1,295	1,380	2,675

[1]In these years, adults were selected (except in Oct. 1972). Fetuses were not collected in 1968.
[2]No samples in September.

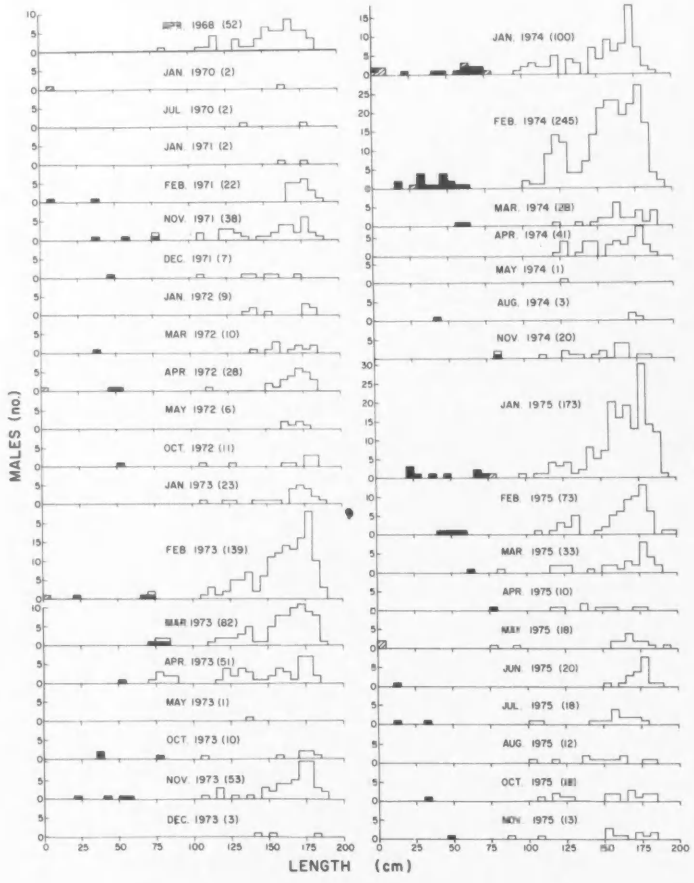

FIGURE 2.—Length-frequency distribution, by 5-cm increments, of collected male eastern spinner dolphins by year and month. Shaded squares are fetuses. Hatched squares are small fetuses of unknown sex (plotted with the males). Sample sizes in parentheses.

Laboratory Procedures

Most laboratory procedures were the same as reported for the earlier study of the growth and reproduction of the spotted dolphin (Perrin et al. 1976). The techniques used in sectioning and reading, however, differed somewhat. Some of the approximately 2,500 teeth prepared (includes recuts, multiple specimens, etc.) were sectioned with multiple cuts, using a high-speed diamond saw

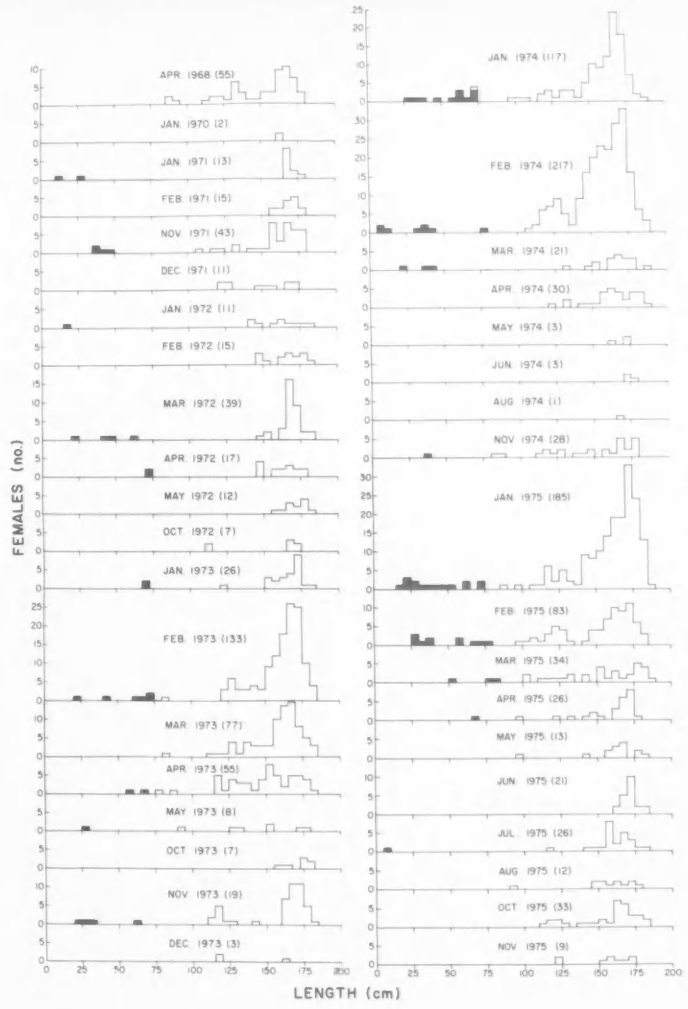

FIGURE 3.—Length-frequency distributions, by 5-cm increments, of collected female eastern spinner dolphins by year and month. Shaded squares are fetuses. Sample sizes in parentheses.

(Felker[6] model 80BQ Hi-speed Precision Cut-off Machine—36,000 rpm) with a single blade, as for *S. attenuata* (Perrin et al. 1976), but most were sectioned with a single cut of tandem blades (yielding a section of uniform 10/1,000-in thickness) with a low speed saw (Isomet model 11-1180 low speed saw—speed variable to 300 rpm). The latter method yielded sections of more uniform thickness and with fewer extraneous surface striations than did the former. After cutting, sections were immediately mounted under coverslips on microscope slides in balsam, omitting the clearing step used for the *S. attenuata* teeth. Our reading and scoring methods also differed from those in the earlier study. We found postnatal dentinal growth to be much more consistent in *S. longirostris* than in *S. attenuata* in pattern of deposition and in readability. No teeth were encountered that did not contain an open cavity, albeit in older specimens a very small one, and a smaller proportion of teeth from younger animals (<12 to 13 layers) contained convoluted secondary dentine than in *S. attenuata*. In the study of *S. attenuata*, growth

[6]Reference to trade names does not imply endorsement of the product by the National Marine Fisheries Service, NOAA.

layers were merely counted to the nearest half layer. In view of the better readability of the *S. longirostris* material, we felt that the approach could be refined. We measured the thickness of each growth layer on an image projected on a 16-cm diameter ground-glass screen attached to a compound microscope using dial calipers accurate to 0.1 mm. The total magnification on the screen was approximately 263 diameters. The first two layers inside the neonatal tooth were measured at approximately the same point along the length for each tooth, about halfway between the proximal end of the neonatal tooth (point where neonatal line meets outer surface) and the distal end of the neonatal pulp cavity. Layers beyond the second were measured at the place along the length of the tooth where they were most clearly defined. In converting measurements to layer units, non-innermost layers beyond the first layer were scored as full layer units regardless of thickness. The first layer, second (when innermost), and subsequent layers (when innermost) were treated differently, as follows:

First Layer

Cumulative percent of 417 first layers measured rapidly approaches an asymptote at approximately 0.20 mm (Figure 4). A first layer 0.20 mm thick or thicker was therefore scored as a full layer unit, and the thickness of a first layer <0.20 mm thick was divided by 0.20 mm to yield a partial layer unit.

Second Layer

In 361 teeth with three or more layers, the second layer averaged 0.145 mm thick with relatively low variance (Figure 5). In teeth with two layers, the second layer was scored as a full layer unit if 0.145 mm thick or thicker. An innermost second layer <0.145 mm thick was scored as a partial layer unit by division of the thickness by 0.145 mm.

Layers Beyond Second Layer

Full layers beyond the second layer averaged more than 95% of the thickness of the next older, adjacent layer, with considerable variation that increased toward the center of the tooth (Figure 6). We assumed, as a reasonable approximation, that complete layers beyond the third are of about the same thickness as adjacent layers, and thickness of the innermost layer in teeth with three or more layers was scored as a proportion of the next older, adjacent layer. Layer scores thus obtained were added and rounded off to the nearest tenth of a layer.

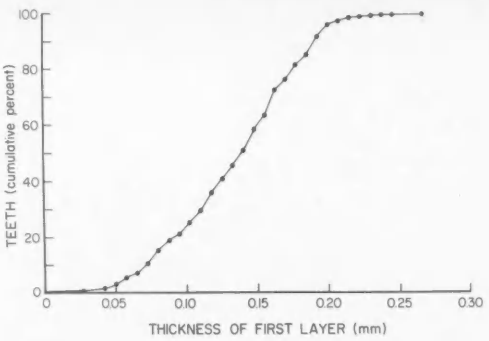

FIGURE 4.—Cumulative percent of first growth layers in relation to thickness of layer in the teeth of 417 eastern spinner dolphins showing asymptote of sigmoid curve at about 0.20 mm.

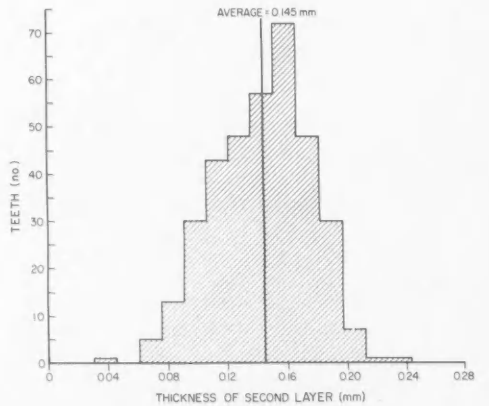

FIGURE 5.—Frequency distribution of thickness of second growth layer in teeth of 361 eastern spinner dolphins.

Brain weights were obtained from brains dissected out of freshly thawed heads or whole carcasses of specimens deep frozen at sea aboard tunaboats, except for nine weights for *S. attenuata* (two fetuses, two neonates, and four adults) obtained from George A. Sacher (Argonne National Laboratory, Argonne, Ill., pers. commun.).

Testes were weighed with the epididymes attached.

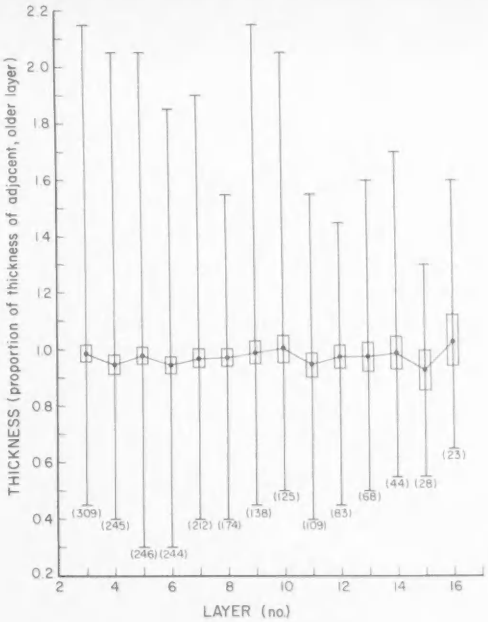

FIGURE 6.—Thickness of growth layers, beyond second postnatal layer, in teeth of the eastern spinner dolphin as proportion of thickness of next older, adjacent zone. Box is one SD on each side of mean; vertical line is range; sample size in parentheses.

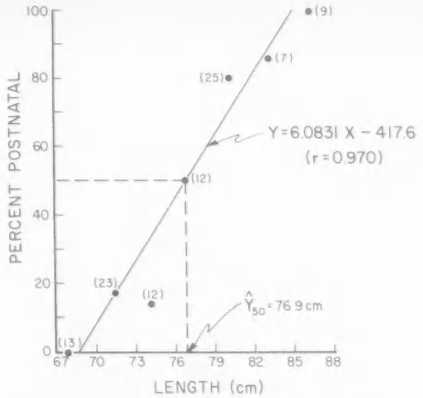

FIGURE 7.—Estimation of average length at birth, based on weighted linear regression of percent postnatal on body length, in 3-cm increments, for 101 specimens of *Stenella longirostris* (54 fetuses and 47 neonates) between 67 and 88 cm long.

RESULTS

Growth

Length at Birth

The largest fetus encountered was 84 cm long. The smallest free-swimming calf was 70 cm long. Estimated average length at birth is 76.9 cm. The estimate is based on a weighted linear regression of percent postnatal on body length, for 3-cm groupings, of 101 specimens (54 fetuses and 47 neonates) between 67 and 99 cm long (Figure 7) collected in random samples. Because of the small sizes of the available samples, 23 specimens of the whitebelly form (11 neonates and 12 fetuses) and 23 specimens unidentified to geographical form (16 neonates and 7 fetuses) were included. This is justified because of the small difference in length of adults of the two forms (<5 cm—Perrin 1975a). Such a difference could be expected to translate into a probable error in the estimate of length at birth, based on the present sample composition, of <0.5 cm, less than that to be expected to be introduced by reduction of the sample size (by 47%) through restriction to specimens known to be eastern spinner dolphins. The estimate is rounded off to 77 cm in analyses below.

This method of estimating average length at birth assumes that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. It also assumes equal rates of prenatal and postnatal natural mortality and assumes that the stresses imposed by pursuit and capture do not cause premature births during the chase or in the net. It was not possible to test these assumptions although some evidence indicates that the last may not be justified (see discussion below in The Calving Cycle and Pregnancy Rate).

Length of Gestation and Fetal Growth

The usual method used to estimate length of gestation is that of Laws (1959), in which progression of a mode in fetal lengths is followed through the seasons. This method was used to estimate length of gestation for the spotted dolphin (Perrin et al. 1976). The method could not be applied to the present samples of data for the eastern spinner dolphin, however. Although breeding is perhaps synchronous at some level (e.g., note peaks in the length–frequency distributions for postnatal males and females in February and April 1973, and February 1974—Figures 2, 3), progression of

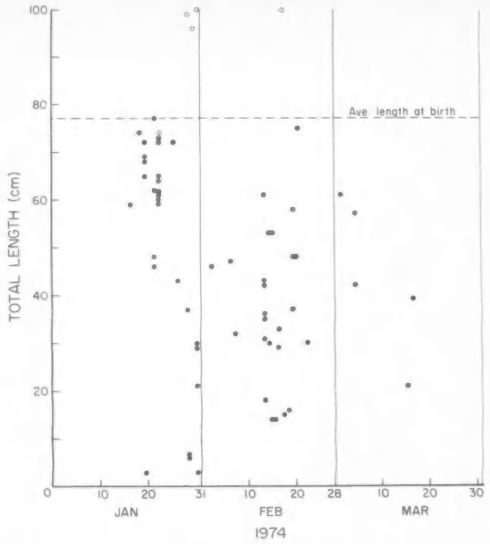

FIGURE 8.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-March 1974.

fetal modes is not apparent in the data. For example, in the large samples of fetuses collected in January–March 1974 (Figure 8), a sharp mode at 60 to 75 cm in January is not apparent in February, even as neonates, and the diffuse mode at 30 to 60 cm in February is not accounted for in the January sample. A probable reason for these discrepancies is the existence of area-related differences in the timing of calving peaks or in the degree of synchrony of breeding. The tuna fleet, our source of samples, moves around from month to month. The January 1974 samples came for the most part from more easterly, offshore localities than did the February samples (Figure 9). In other words, in 1974, calving in the more offshore region may have been sharply synchronized, with a peak in February–March, while in the more onshore region, calving may have been spread over most of the year. This hypothesis is reinforced by the data for January–April 1975, when sizeable samples of fetuses were collected in the more onshore region during both January and February and smaller samples through April (Figure 10) were from more offshore (around Clipperton Island), northerly

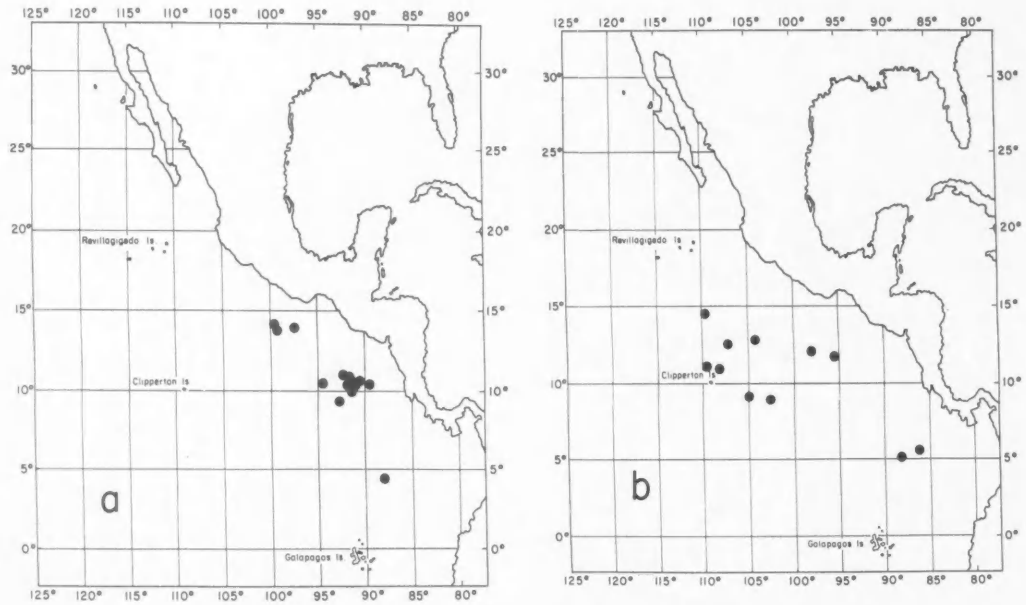

FIGURE 9.—Localities at which fetuses of the eastern spinner dolphin were collected in January (a) and February (b) 1974.

(Revillagigedos Islands), or southerly (near the Equator, east of the Galapagos Islands) regions. Even if only onshore samples are considered (those circled in Figure 10), there is no clear pattern of progression of fetal length modes (Figure 11). It is, of course, possible that the size of the population unit within which breeding is synchronous may be smaller than suggested by the onshore-offshore comparison. In any case, this complexity makes impossible the use of Laws' method for estimating gestation based on aggregated samples, and stratification of the data to even smaller areas than used above yields samples too small for meaningful analysis. For these reasons, we attempted to estimate length of gestation by two other, less direct methods: a) on the basis of relative length at birth compared with that of other, closely related delphinids for which estimates of gestation period exist, and b) on the basis of a recently discovered empirical relationship between brain size parameters and gestation in mammals.

ESTIMATE FROM COMPARISON WITH OTHER DELPHINIDS BASED ON LENGTH AT BIRTH.—Estimates of length of gestation derived by comparable methods are available for four delphinids, sensu stricto (Table 2). There is a positive correlation among these closely related forms between length of gestation and length at birth (Figure 12). Extrapolation of this relationship to

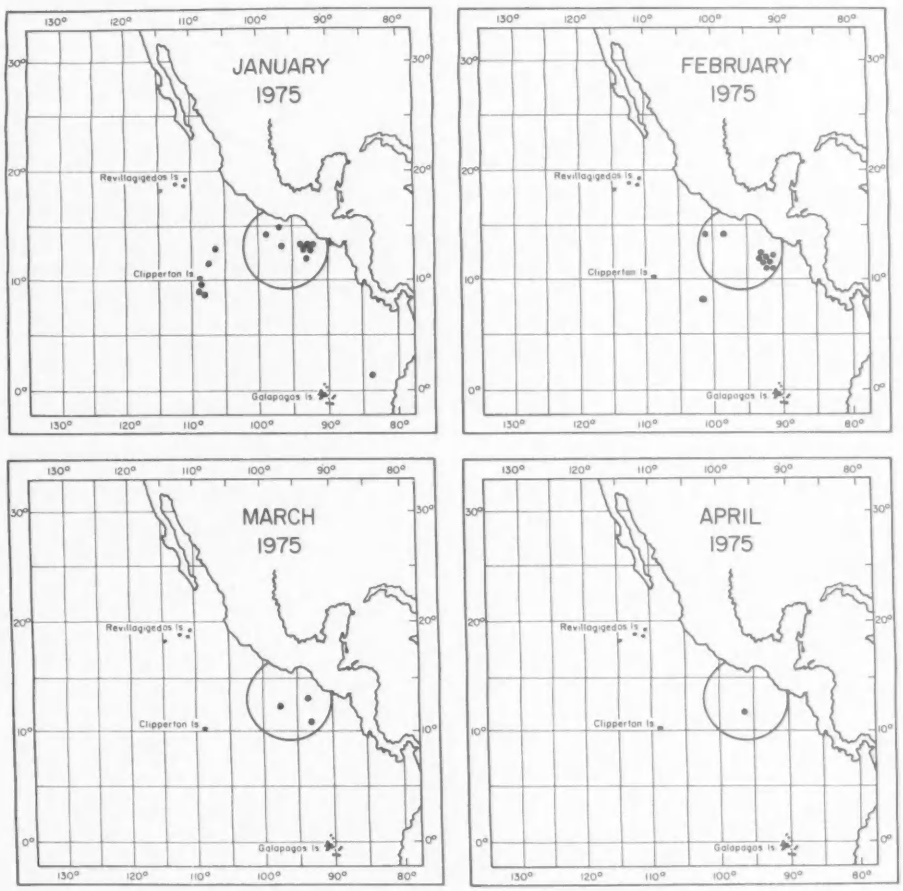

FIGURE 10.—Localities at which fetuses of the eastern spinner dolphin were collected, January-April 1975.

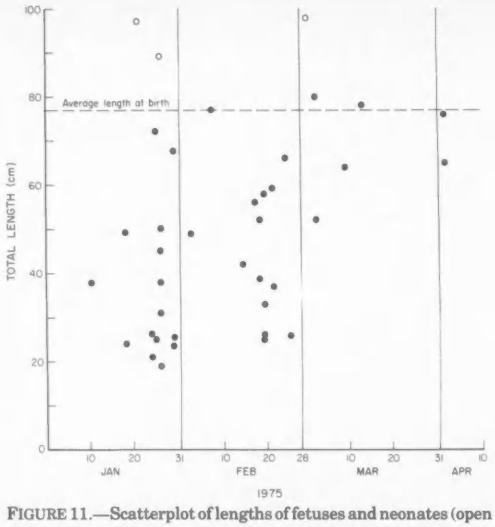

FIGURE 11.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-April 1975 (specimens from localities circled in Figure 10).

TABLE 2.—Estimated average length at birth and length of gestation in four delphinids. Data for *Globicephala* from Sergeant (1962), for *Tursiops* from Sergeant et al. (1973), for *Stenella coeruleoalba* from Kasuya (1972), for *S. attenuata* from Kasuya et al. (1974) (off Japan) and from Perrin et al. (1976) (eastern Pacific). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975).

Species	Length at birth (cm)	Gestation (mo)
Long-finned pilot whale	176.0	15.75
Globicephala melaena	(average of males	(15.5-16.0)
(Newfoundland)	and females)	
Bottlenose dolphin	100.0	12.0
Tursiops truncatus		
(northeast Florida)		
Striped dolphin	99.8	12.0
Stenella coeruleoalba		
(off Japan)		
Spotted dolphin		
Stenella attenuata		
a. (off Japan)	89.0	11.2
b. (eastern Pacific)	82.5	11.5

length at birth for *S. longirostris* of 77 cm yields a deduced length of gestation of 10.74 mo (325 days).

ESTIMATE BASED ON GROWTH PARAMETERS OF THE BRAIN.—Sacher and Staffeldt (1974) recently demonstrated an empirical relationship between gestation time and brain weight in placental mammals. This relationship explains more of the wide variation in mammalian gestation times than do previous empirical approaches involving body size parameters, such as cube root

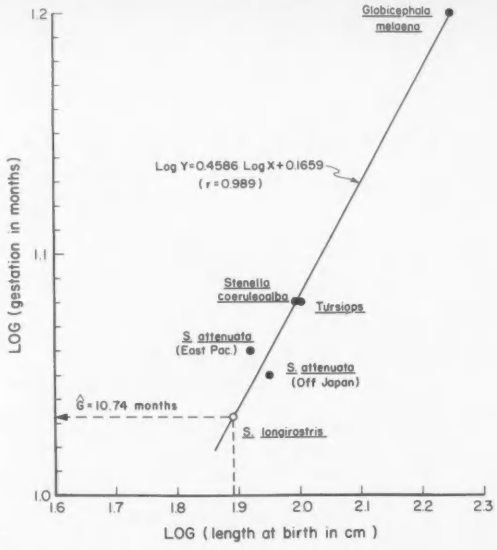

FIGURE 12.—Relationship between log of length of gestation and log of length at birth in four delphinid cetaceans, with extrapolation to predicted length of gestation in the eastern spinner dolphin.

of weight at birth (Huggett and Widdas 1951) or length at birth (as in above estimate). They developed a predictive equation based on linear multiple regression analysis:

$$\log G = 0.274 \log E_n + 0.144 \log A_e + 0.173 \log N + 1.853$$

where G = gestation time in days
E_n = neonatal brain weight in grams
A_e = "brain size advancement," or ratio of neonatal to adult brain weight
N = litter size (1 in cetaceans).

Application of this equation to brain data for *S. longirostris* (Figure 13—neonatal brain weight = 231 g, adult brain weight = 465 g) yields an estimate of gestation time of 286 days (9.45 mo). The method has not yet been tested on a significant number of delphinid species for which gestation time has been more directly estimated,[7] and we

[7]The estimates used by Sacher and Staffeldt of brain weight at birth and adulthood for *Tursiops* are from Lilly (1967) and are based on samples of unstated and probably small size, a very important consideration in light of the large individual variation in these features (Figures 15, 16) and geographical variation in overall size (Anonymous 1975). For example, eight *Tursiops* brain weights summarized by Gihr and Pilleri (1969) averaged

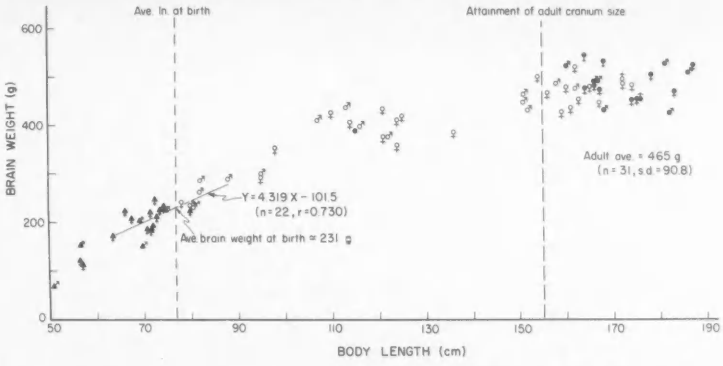

FIGURE 13.—Scatterplot of brain weight on body length for 77 specimens of *Stenella longirostris* from the eastern Pacific. The sample of fetuses and neonates (<100 cm) includes 11 eastern spinner dolphins, 9 whitebelly spinner dolphins, and 9 specimens (mostly fetuses) unidentified to race. Triangles are fetuses, open circles are sexually immature postnatal specimens, shaded circles are sexually adult specimens (by criteria explained in text below). Length at attainment of adult cranium size based on data in Perrin (1975b). The linear regression to estimate brain weight at birth is based on 22 near-term fetuses and neonates 63 to 88 cm long.

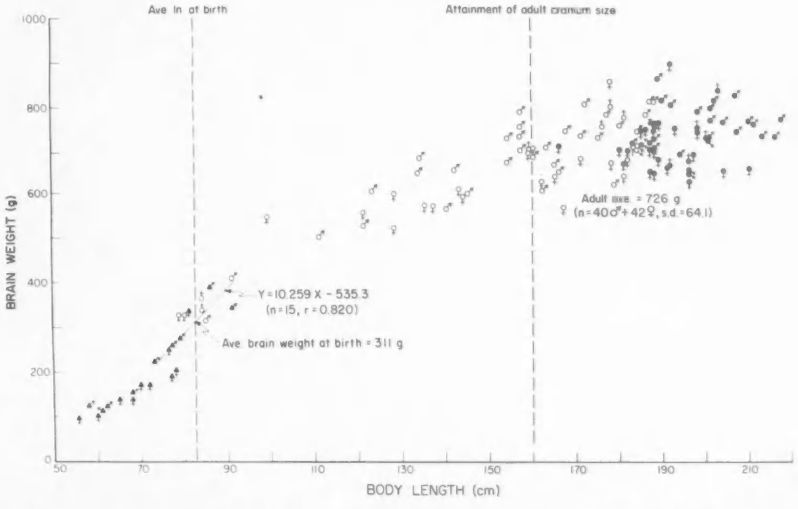

FIGURE 14.—Scatterplot of brain weight on body length for 133 eastern spinner dolphins from the offshore eastern tropical Pacific. Triangles are fetuses, open circles are sexually adult specimens. Linear regression to estimate brain weight at birth based on near-term fetuses and neonates, 73 to 91 cm long. Criteria for sexual maturity and basis for length at attainment of adult cranium size from Perrin (1975b).

1,475 g, compared with the 1,600 g reported by Lilly based on an unknown sample size. Twelve nonneonatal brain weights (probably including some of juveniles) published by Morgane and Jacobs (1972) ranged from 1,260 to 1,950 g and averaged 1,536 g. Thus, deviation of the estimate of Sacher and Staffeldt for *Tursiops* (396 days, or 13.08 mo) from the more directly obtained estimate of 12 mo (Sergeant et al. 1973), an overestimate of about 10%, is of unknown significance and probably reflects statistical error as well as possibly deductive error.

therefore applied the equation to brain data for the spotted dolphin, *S. attenuata* (Figure 14—neonatal brain weight = 311 g, adult brain weight = 726 g). The estimate of gestation time obtained is 304 days, or 10.03 mo, as compared with 11.5 mo (rounded off) estimated by a more direct method

(Perrin et al. 1976). If it be assumed that some factor in delphinid growth is unaccounted for in the Sacher-Staffeldt model and that gestation time for *S. longirostris* is underestimated to a similar degree (11.5 mo minus 10.0 mo/11.5 mo, or 13%), an adjusted Sacher-Staffeldt estimate of 10.54 mo is obtained.

The estimate based on length at birth (10.74 mo) and the adjusted Sacher-Staffeldt estimate (10.54 mo) are close to each other, and a rounded off average of the two estimates, 10.6 mo, is used below in the analyses of reproduction. Making the assumption that fetal growth follows a pattern similar to that in *S. attenuata*, i.e., that t_0 in Laws' fetal growth equation $L = a(t - t_0)$ is approximately the same proportion of gestation time as in *S. attenuata*, or 0.135 t_g (Perrin et al. 1976), a fetal growth curve can be estimated (Figure 15). The slope of the linear portion of the curve is 8.367 cm/mo, as compared with 8.283 cm/mo estimated for *S. attenuata* (Perrin et al. 1976).

Postnatal Growth

We found it impossible to estimate postnatal growth rates by the usual method of following the seasonal progression of length modes, for the reasons discussed above. We deduced an estimate of growth rate during the first 10 to 11 mo by application of the equation, $\log Y = 0.99 \log X - 1.33$, expressing an inferred relationship in toothed cetaceans between length at birth (X above) and the difference (Y above) between the growth rates during the linear phases of fetal and early postnatal growth (Perrin et al. 1976). The predicted difference based on length at birth of 77 cm is 3.60 cm/mo. Subtraction of this from the fetal linear growth (estimated above) of 8.37 cm/mo yields an estimate of average growth rate during the first 10 to 11 mo after birth of 4.77 cm/mo. If this is taken as an estimate of average growth rate during the first year, predicted length at 1 yr is 134 cm. This method overestimates length at 1 yr to some unknown, but slight extent, as growth is only approximately linear in the first year.

FIGURE 15.—Estimated fetal growth curve for the eastern spinner dolphin.

We examined the relationship between length and number of postnatal dentinal growth layers in the teeth for 183 males and 250 females (Figure 16). The occurrence in the samples of length-layer data for relatively more females than males with more than about 12 layers is accounted for by the fact that the sample of males selected for tooth-sectioning was stratified entirely by length, whereas the sample of females was stratified by length in juveniles and by number of ovarian corpora in adults. All females with more than 10 ovarian corpora were included in the sample, in addition to randomly selected, corpora-stratified subsamples of females with <10 corpora.

We fit growth curves to the data (to single-layer incremental means), using a two-cycle version of the Laird growth model (see Perrin et al. 1976 for discussion of the model). Juvenile males and females were considered jointly. The fit was forced through the origin (zero growth layers, and estimated length at birth of 77 cm), and asymptotic length (L_∞) was estimated as the average length of animals with 13 or more layers (L_∞ for 12 males = 179.46 cm and for 60 females = 170.91 cm), fixing the upper ends of the two curves of the second cycle. The simultaneous iterative fitting procedure arrived at 4.111 growth layers (rounded off to 4 below) as the age at which convergence of the three curves (estimated onset of a secondary growth spurt) yields the best fit (Figure 16). Estimated length at this age is 156.85 cm. The Laird/Gompertz model (Laird 1969) is

$$L(t) = L_0 \exp\left\{\frac{a}{\alpha}\left[1 - \exp(-\alpha t)\right]\right\}$$

where L = length in centimeters
t = age
L_0 = length at age zero
a = specific rate of exponential growth
α = rate of decay of exponential growth.

A form of the model generalized to the present case of more than one cycle is

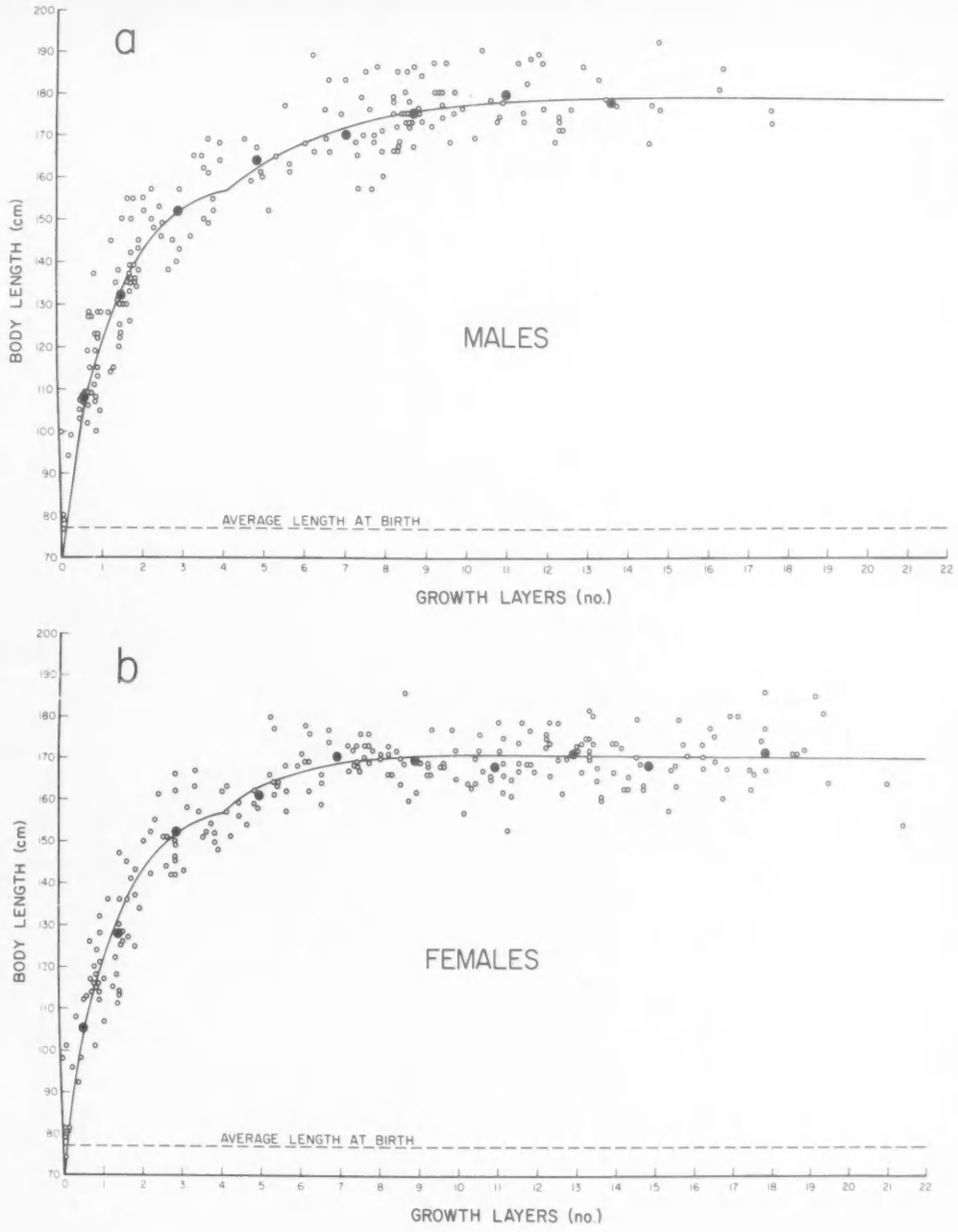

FIGURE 16.—Scatterplot of body length on number of postnatal dentinal growth layers in 183 male (a) and 250 female (b) eastern spinner dolphins. Circled dots are means for 0-1 layer, 1-2 layers, for 2-layer increments thereafter until 12 layers in males and 16 in females and for ≥12 layers and ≥16 layers, respectively. The line is a two-cycle Laird fit to single-layer incremental means (see text).

$$L(t) = L' \exp\left\{\frac{a}{\alpha}\left[1-\exp(-\alpha(t-t'))\right]\right\}$$

where L' = length (centimeters) at start of cycle
t' = age (growth layers) at start of cycle.

The growth equation for juveniles of <4 growth layers is

$$L = 77 \exp\left\{\frac{0.6630}{0.9098}\left[1-\exp(-0.9098t)\right]\right\}.$$

The growth equation for males of >4 growth layers is

$$L = 156.85 \exp\left\{\frac{0.0507}{0.3765}\left[1-\exp(-0.3765(t-4.11))\right]\right\},$$

and for females

$$L = 156.85 \exp\left\{\frac{0.0546}{0.6354}\left[1-\exp(-0.6354(t-4.11))\right]\right\}.$$

The fits of the model to both males and females is excellent, albeit slightly better for the females about the point of convergence of the two curves than for males.

The equations rearranged and reduced for estimating age from length are

♂ and ♀ < 157 cm

$$t = -1.099 \ln(6.960 - 1.372 \ln L)$$

♂ > 157 cm

$$t = 4.113 - 2.656 \ln(38.540 - 7.426 \ln L)$$

♀ > 157 cm

$$t = 4.113 - 1.574 \ln(59.871 - 11.645 \ln L).$$

Note: These equations should not be used to estimate age from actual length data except for grouped samples of smaller animals (about 165 cm or less in females and 170 cm in males), for which growth rate is still large compared with individual variation in length.

Estimated age in growth layers at 134 cm, the predicted length at 1 yr derived above from extrapolative comparison with other delphinids, is 1.57 layers. Since, as discussed above, the estimate of 134 cm is likely to be a slight overestimate due to some nonlinearity of growth during the first year, the estimate of 1.57 layers is rounded down (to the nearest half layer) to 1.5 layers for use below in the various hypotheses of rate of accumulation of layers.

It appears that, effectively, in terms of the data yielded by the tooth readings, 1.5 layers are laid down in the first year. One possible explanation alternative to that of actual deposition of 1.5 layers/yr is that a single layer is laid down in the first year, but that in some individuals (about half) there is a strongly developed subsidiary line within the layer that makes the single layer appear like two layers, yielding an average of 1.5 layers. This explanation seems unlikely, however, in view of the data on thickness of the first layer.

The "subsidiary line" hypothesis would predict a subsidiary inflection or plateau in the cumulative percent of first layers in relation to thickness, and such is not apparent (Figure 4).

We found no correlation between thickness of the innermost growth layer and month of capture (Table 3). It is apparent from the data that the layers are formed rapidly (very few relatively thin innermost layers are seen) and probably throughout the year in the population.

With no basis for direct calibration, we provisionally use three alternative hypotheses of rate of layer deposition (similar to those put forth for the spotted dolphin, *S. attenuata*—Perrin et al. 1976) in the age-based analyses below, namely:

I. One and one-half layers per year, or

TABLE 3.—Thickness of innermost growth layer in teeth of 331 eastern spinner dolphins, with 3-12 layers, by month of capture.

Month	Sample size (no.)	Thickness of innermost layer ÷ thickness of next youngest layer: Average (%)	Minimum (%)	Maximum (%)
Jan.	38	90.1	65	100
Feb.	107	83.3	20	100
Mar.	42	88.3	30	100
Apr.	13	81.1	50	100
May	9	89.9	67	100
Aug.	3	98.0	94	100
Oct.	7	71.1	47	100
Nov.	26	83.6	44	100
Dec.	5	94.0	73	91

II. One and one-half layers in the first year and one per year thereafter, or
III. One and one-half layers per year until puberty (at about nine layers in males and five to six layers in females) and one per year thereafter.

There is a rapidly increasing body of evidence (Perrin et al. 1976; Best 1976) that most delphinids accumulate growth layers at the rate of 1/yr, making Hypothesis II the most likely true of the three, but some uncertainty still exists, especially for tropical forms. We therefore express the conclusions of all age-based analyses below in terms of the three hypotheses. Other, more complex hypotheses can be suggested, but these three in our view probably include the truth.

Reproduction

The Male

Spermatogenesis is histologically evident in 50% of (right) testes weighing 94 g or more (weight of epididymis included) (Figure 17). A perhaps better criterion of sexual maturity is presence of sperm in the epididymis (Figure 18). Combined testis-epididymis weight at which half the males possess "some" or "copious" sperm in the epididymis is approximately 150 g. Another epididymal criterion can be defined, namely, the testis-epididymis weight above which the proportion of males having "copious" sperm in the epididymis does not increase, in this case above 50% at about 400 g. The three testis-epididymis weight criteria of 94 g (50% spermatogenic), 150 g (50% with sperm in epididymis), and 400 g (asymptotic weight with respect to proportion with copious sperm) are considered below in relation to body length and age (in dentinal growth layers).

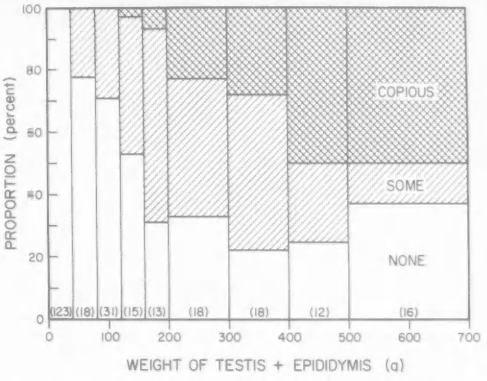

FIGURE 18.—Presence of sperm in epididymis in relation to testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

Testis-epididymis weight on the average increases precipitously with body length between 160 and 170 cm (Figure 19), but is only weakly correlated with body length beyond 175 cm. Males of any length above 160 cm can be mature or immature under each of the three criteria defined above. The proportion of males mature under the three criteria stabilizes at about 170 to 175, 175 to 180, and 180 to 185 cm body length, respectively (Figure 20). The average length of adult males under the three criteria ranges from 174 to 176 cm (Table 4).

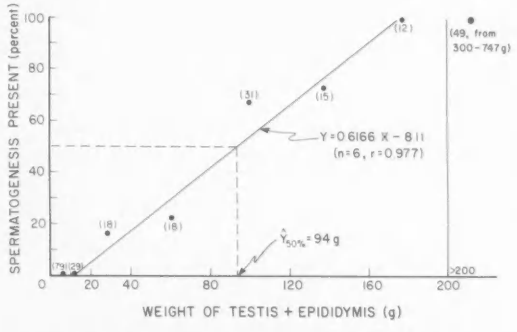

FIGURE 17.—Linear regression analysis of relationship between proportion of males spermatogenic and testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

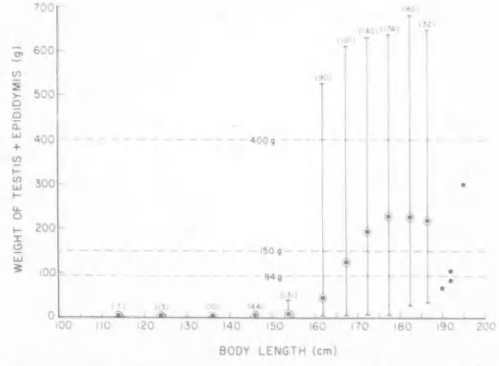

FIGURE 19.—Relationship between testis-epididymis weight and body length in the eastern spinner dolphin. Circled dots are sample means. Vertical bars are ranges. Sample sizes in parentheses.

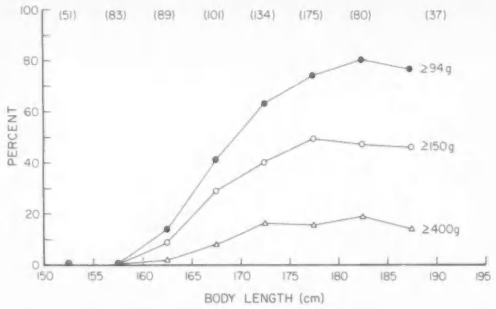

FIGURE 20.—Proportion of males sexually mature in relation to body length in the eastern spinner dolphin under three criteria of testis-epididymis weight. Sample sizes in parentheses.

TABLE 4.—Body length of adult male eastern spinner dolphins under three criteria of sexual maturity.

Weight of testis and epididymis (g)	Sample size (no.)	Body length (cm)			
		Minimum	Maximum	Average	SD
<94	594	108	192	—	—
≥94	356	160	195	176.0	5.99
≥150	230	160	195	175.8	6.06
≥400	81	162	190	174.1	5.79

Testis-epididymis weight is more closely correlated with age (in dentinal growth layers) than with body length (Figure 21). The 94-g level is reached on the average at about 9 growth layers and attained by all males with more than 12 layers. The 150-g level is reached at about 10 layers on the average and by all males at about 13 layers. The 400-g level is reached on the average at about 12 layers, but the oldest male examined (16.5 layers) had a testis-epididymis weight of only 333 g. Estimated average age in years at sexual maturity under the three criteria and under the three layer/year hypotheses ranges from 6.0 to 11.5 yr (Table 5), with the most likely estimates (Hypothesis II) 8.5 to 11.5 yr.

The question of age at attainment of social maturity (sense of Best 1969) in the spinner dolphin must await studies of social structure and breeding patterns. Other (larger) odontocetes, such as the sperm whale, *Physeter catodon*, and the long-finned pilot whale, *Globicephala melaena*, are known or thought to be polygynous, to varying degrees, but the social structure of the spinner dolphin is as yet unknown.

No systematic seasonal variation in testis weight or condition was detected, although the heavy bias in seasonal coverage of the sample precludes an adequate evaluation of this factor.

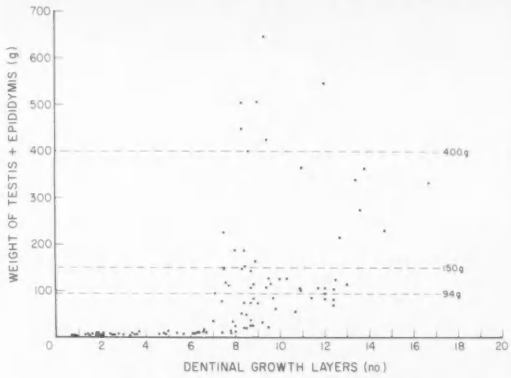

FIGURE 21.—Scatterplot of testis-epididymis weight on age (in dentinal growth layers) for 106 eastern spinner dolphins.

TABLE 5.—Estimated average age in years at attainment of sexual maturity in male eastern spinner dolphins under three criteria of maturity and three growth layer hypotheses. [See text for definition.]

Testis-epididymis criterion (g)	Age (years) under growth layer hypotheses		
	I	II	III
94	6.0	8.5	6.0
150	6.7	9.5	7.0
400	8.0	11.5	9.0

The Female

ATTAINMENT OF SEXUAL MATURITY.—The smallest sexually mature female in the present sample was 152 cm long. The largest immature female was 182 cm long. One estimate of average length at attainment of sexual maturity is the length at which 50% of the females show evidence of having ovulated, i.e. possess ovaries with one or more scars (corpus luteum or corpus albicans). This length in the present sample of eastern spinner dolphins is estimated at 164.1 cm (Figure 22).

The sigmoid curve in Figure 22 is slightly asymmetrical, that is to say, there are more immature animals (91) above the 50%-mature length of 164.1 cm than there are mature animals below it (62). At 165 cm, the numbers are 80 and 77, respectively. This length, 165 cm, is used below to classify as sexually mature or immature specimens for which ovarian data are lacking. The predicted number of growth zones (from the growth equation) at this length is 5.5.

Average age at attainment of sexual maturity can also be estimated directly from the smaller sample of females for which teeth were sectioned (n = 247). This analysis (Figure 23) estimates

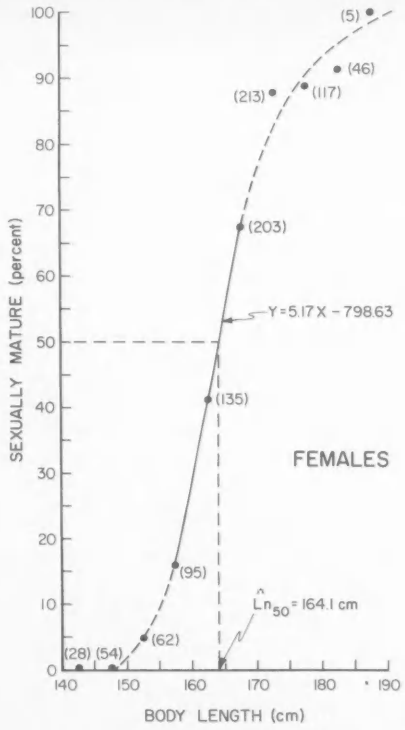

FIGURE 22.—Estimation of body length at which 50% of female eastern spinner dolphins show ovarian evidence of sexual maturity (one or more scars). Fit to central portion of curve (solid line) is linear regression. Dashed portions of curve fitted by eye. Sample sizes in parentheses.

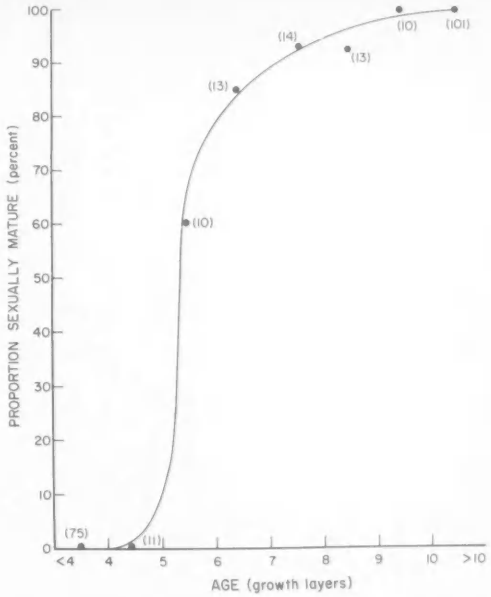

FIGURE 23.—Relationship between proportion of females sexually mature and age, in dentinal growth layers, in the eastern spinner dolphin. Fit is by eye.

average age at attainment of maturity at about 5.4 growth layers, in close agreement with the estimate derived from the age/length equation. A rounded-off average of 5.5 layers is used below. Average age in years at attainment of maturity under the three hypotheses of layer deposition rate are 3.7, 5.0, and 3.7 yr, respectively, with the second estimate being most probably correct.

Sexually adult females in the sample ranged from 152 to 187 cm and averaged 171.2 cm in length (Figure 24).

DISTRIBUTION OF CORPORA TO LEFT AND RIGHT OVARIES.—As in all other odontocetes so far studied, the left ovary predominates in ovulation. As in the case of *S. attenuata*, the distribution between left and right side (Table 6) can be accounted for by assuming that about 90 to 95% of the females ovulate the first time from the left ovary, and the remainder from the right, and that

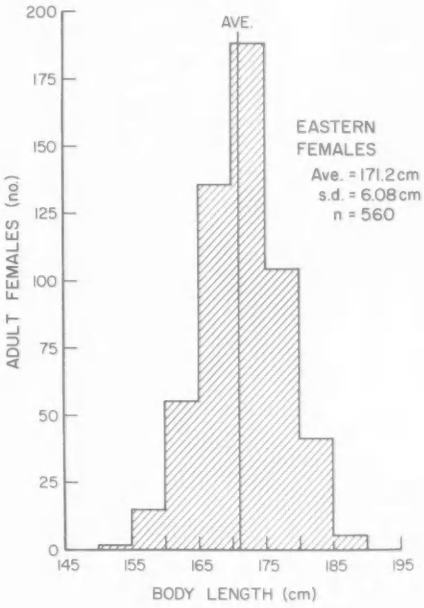

FIGURE 24.—Length-frequency distribution of 560 sexually adult (possessing at least one ovarian corpus) female eastern spinner dolphins.

TABLE 6.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 556 eastern spinner dolphins.

Corpora (no.)	Sample size (no.)	Location of corpora: Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	41	92.7	7.3	—
2	51	78.4	9.8	11.8
3	50	92.0	2.0	6.0
4	43	90.7	2.3	7.0
5	56	91.1	3.6	5.3
6	53	86.8	11.3	1.9
7	60	85.0	15.0	0.0
8	39	82.1	10.3	7.6
9	26	80.8	11.5	7.7
10-11	63	73.0	19.0	8.0
12-15	55	41.8	1.8	56.4
16-19	13	23.1	0.0	76.9
20-26	6	16.7	0.0	83.3

succeeding ovulations are from the same ovary (left or right) about 90 to 95% of the time. When about 10 corpora have accumulated, emphasis shifts sharply to the opposite ovary.

OVULATION RATE.—The number of ovarian corpora, including corpora lutea, ranged from 1 to 26 in 555 sexually adult females. The frequency distribution (Figure 25) is very similar in shape to that for *S. attenuata* (Perrin et al. 1976) with highest frequencies at 5 to 7 corpora and a sharp falloff after about 10 corpora.

Size-frequency distribution of the various types of corpora albicantia among the corpora-type categories relative to total number of corpora were the same in this sample as in the sample of *S. attenuata* previously studied (Perrin et al. 1976) leading us to believe that, for this species also, corpora of ovulation persist throughout the life of the animal, accumulating at Type 3.

Scatter in a plot of number of corpora on age in growth layers is wide (Figure 26) but not as great as encountered in a study of *S. attenuata* (Perrin et al. 1976). Factors producing the scatter are 1) error in reading growth layers, 2) individual variation in ovulation rate, and 3) change in ovulation rate during the reproductive span. The teeth of *S. longirostris* in this study had more clearly defined, more easily readable growth layers than did those of *S. attenuata* in the previous study, and this probably accounts for the relatively less scatter for the former, although less influence by either or both of the other two factors cannot be ruled out.

Calculation of average ovulation rates from the data in Figure 26 must take into account individual variation in age at first ovulation. The data were grouped into 2-layer intervals (all those with 12 or more layers were included in a single final increment), and average reproductive age by interval P calculated as

$$\bar{A} = \frac{\sum_{i=1}^{P} a_i b_i}{c_i}$$

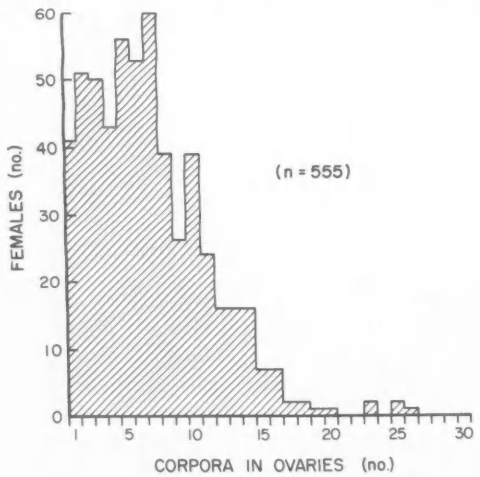

FIGURE 25.—Frequency distribution of ovarian corpora count in 555 female eastern spinner dolphins.

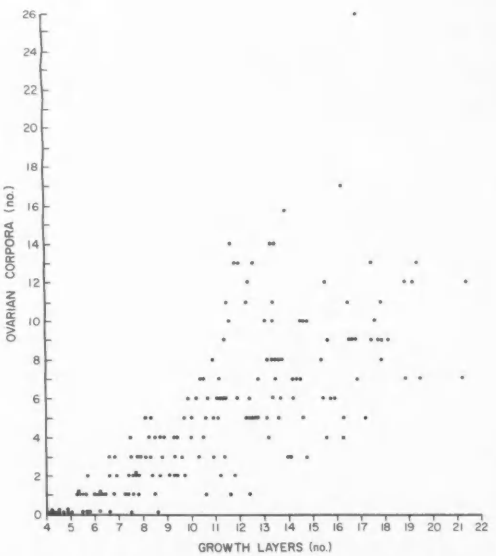

FIGURE 26.—Scatterplot of number of ovarian corpora on age, in dentinal growth layers, in 1,972 female eastern spinner dolphins.

where a_i = percent maturing in ith interval (percent maturing in i minus percent maturing in $i - 1$)
b_i = average reproductive age in interval P of females maturing in i
c_i = percent mature in interval P.

Average reproductive age in the ith interval of females maturing in i was set at 0.50 layer. A plot of number of ovulations on average reproductive age (Figure 27) shows linear increase, with a slope of unity (one ovulation per layer), in number of corpora until about 10 corpora have been accumulated at about 10 layers of reproductive age (15.5 layers total age on the average) when the ovulation rate apparently drops sharply. This is very different from the results obtained in a similar best-fit analysis for *S. attenuata* (Perrin et al. 1976), which indicated average ovulation rates of about four during the first layer, two during the second, and about one per layer thereafter. A power fit to the data for *S. longirostris* (Figure 27) shows much less variation in ovulation rate with age. It appears that in the presently sampled population of *S. longirostris* there is less multiple infertile ovulation in very young mature females than in the studied population of *S. attenuata*. This may be an inherent difference or may reflect differential status of the two populations with respect to exploitation. For example, females could on the average become sexually mature at an earlier age in an exploited population but be less fertile, in terms of pregnancies per ovulation, than had they become mature at greater age. Estimated ovulation rates were higher in the studied eastern Pacific population of *S. attenuata* than in a relatively unexploited population of the same species in Japanese waters (Perrin et at. 1976).

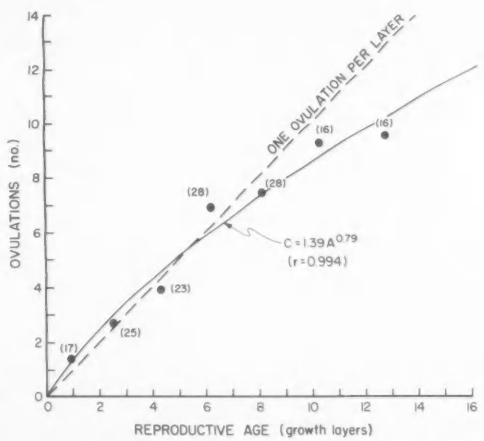

FIGURE 27.—Scatterplot of 2-layer means (last mean is for 12-16 layers) of average number of ovulations on average reproductive age in growth layers in the eastern spinner dolphin. Regression line is power fit. One-ovulation-per-layer line added. Sample sizes in parentheses.

POSTREPRODUCTIVE FEMALES.—Four adult females of 536 examined (≈1.0%) showed clear evidence of being postreproductive, or "senile," by criteria of 1) being inactive, or "resting" (neither pregnant nor lactating); 2) having high corpora count (≥10); 3) having small, withered ovaries (weighing <3.5 g); 4) having no developing follicles (largest follicle <1 mm in diameter); and 5) having no Type 1 or 2 corpora albicantia (terminology of Perrin et al. 1976), indicating recent ovarian activity (Figure 28).

THE CALVING CYCLE AND PREGNANCY RATE.—The calving cycle, for purposes of analyzing the types of field data available, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting"—a catch-all "phase" for animals neither pregnant nor lactating, which includes

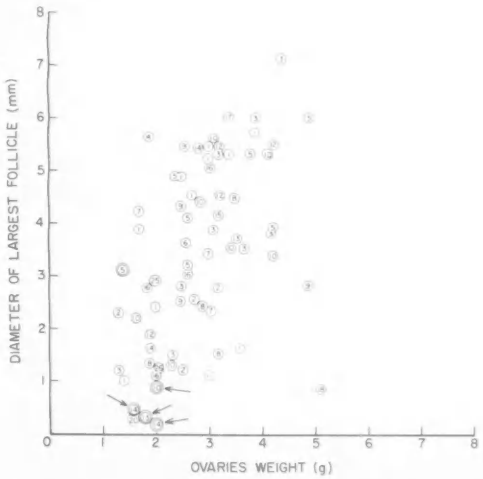

FIGURE 28.—Scatterplot of diameter of largest follicle on combined weight of ovaries for 73 adult female eastern spinner dolphins classified as "resting" (not pregnant or lactating). Specimens with corpora lutea or cystic follicles not included. Number in circle is total number of corpora in ovaries (including corpus luteum). Double circles are specimens with no Types 1 or 2 corpora albicantia indicating recent ovarian activity. Four postreproductive females indicated with arrows.

females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf.

The gestation phase of the cycle was estimated above, at 10.6 mo. We estimated average length of lactation by two methods; 1) by assuming that the proportion of a sample of mature females in a particular reproductive phase is directly proportional to the relative length of that phase in the overall cycle, i.e., that the samples are not biased with regard to reproductive phase (the length of the "resting" phase was also estimated this way); and 2) by assuming that a suckling calf exists for each lactating female, and the samples are unbiased with respect to suckling calves and lactating females, under which assumptions the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length (and, from the growth equation, age) at weaning. The first estimate was based on data for 536 adult females collected 1971–75, classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 7). The resting females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). Only three females were simultaneously pregnant and lactating (1.44% of lactating females).

Subtraction of the postreproductive females and allocation of the females both pregnant and lactating to both of the two categories provides estimates of the proportions of the reproductive females in the three phases of the cycle (Figure 29) and of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, using the estimated gestation

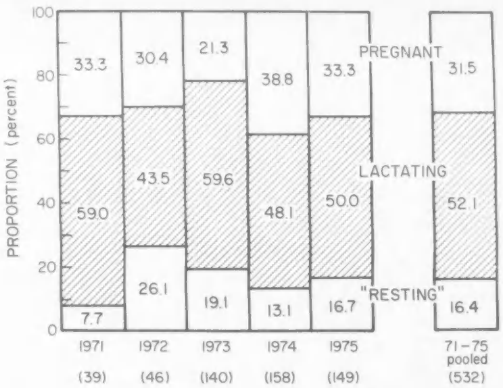

FIGURE 29.—Proportions of 532 adult reproductive female eastern spinner dolphins in pregnant, lactating, and "resting" (not pregnant or lactating) phases of cycle. Based on Table 4. Females both lactating and pregnant alloted to both phases. Postreproductive females excluded.

period of 10.6 mo (Method 1 in Table 8). The estimates of average length of lactation thus derived range from 13.1 to 29.7 mo (the possible causes of this wide year-to-year variation in phase structure of the samples are discussed below in Gross Annual Reproduction), with a pooled average of 17.5 mo.

The second method of estimating length of lactation, the "cumulative calf length/lactating females" method yielded estimates for six single-month samples ranging from 7.7 to 16.0 mo and for single-year samples from 9.4 59 10.6 mo (Method 2 in Table 8). The pooled estimate for 1973-75 is 10.1 mo. The three yearly estimates are consistent with each other and sharply lower than the estimates yielded by the "proportion-in-phase" method above (compare in Table 9). The first method could be invalid and cause disparate estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples, or conversely, 2) either (or both) pregnant or "resting" females were underrepresented. This situation could obtain if lactating females and their

TABLE 7.—Reproductive condition of 536 adult female eastern spinner dolphins collected 1971-75.

	1971		1972		1973		1974		1975		1971-75 pooled	
Condition	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pregnant only	13	33.3	14	30.4	29	20.6	60	37.3	49	32.9	165	30.8
Lactating only	23	59.0	20	43.5	83	58.9	75	46.6	74	49.7	275	51.3
Pregnant and lactating	0	0	0	0	1	0.7	2	1.2	1	0.7	4	0.7
"Resting"												
with corpus luteum	0	0	4	8.7	3	2.1	5	3.1	3	2.0	15	2.8
without corpus luteum	3	7.7	8	17.4	24	17.0	16	9.9	22	14.8	73	13.6
Postreproductive	0	0	0	0	1	0.7	3	1.9	0	0	4	0.7
Total	39	100.0	46	100.0	141	100.0	161	100.0	149	100.0	536	100.0

TABLE 8.—Estimated lengths of postreproductive phases, under two methods of estimating length of lactation, of the eastern spinner dolphin based on single-year samples, 1971-75, and on pooled samples for all years, with estimates of pregnancy rate and calving interval based on lactation estimate 1.

Item	1971	1972	1973	1974	1975	Pooled
Sample size (no.)	39	46	140	158	149	532
Pregnancy (months)	10.6	10.6	10.6	10.6	10.6	10.6
Lactation (months):						
Method 1	18.8	15.2	29.7	13.1	15.9	17.5
Method 2 (Hyp. II)	—	—	10.6	9.4	10.2	10.1 (1973-75)
"Resting" (Method 1)	2.6	9.1	9.5	3.6	5.3	5.5
Sum of phases:						
Method 1						
(months)	32.0	34.9	49.8	27.4	31.8	33.6
(years)	2.66	2.91	4.15	2.28	2.65	2.80
Method 2						
(months)	—	—	26.7	25.5	26.3	26.2
(years)	—	—	2.23	2.13	2.19	2.18
Annual pregnancy rate (APR):						
Method 1	0.375	0.344	0.243	0.444	0.380	0.360
Method 2	—	—	0.450	0.474	0.459	0.461
Calving interval (1/APR):						
Method 1						
(years)	2.66	2.91	4.12	2.25	2.63	2.78
(months)	32.0	34.9	49.5	27.0	31.6	33.4
Method 2						
(years)	—	—	2.22	2.11	2.18	2.17
(months)	—	—	26.6	25.3	26.2	26.1

TABLE 9.—Estimates of length of lactation in the eastern spinner dolphin based on the "cumulative calf length/lactating females" method (see text), for 6 single-month samples and for 1973-75 by year and pooled.

Sample	Lactating females[1] (no.)	Length at which cumulative number of calves = number of lactating females (cm)	Length of lactation (months, under Hypotheses)		
			Layers	I	II and III
Feb. 1973	41	139	1.83	14.6	16.0
Mar. 1973	18	133	1.52	12.2	12.2
Jan. 1974	23	124	1.16	9.3	9.3
Feb. 1974	42	118	0.97	7.7	7.7
Jan. 1975	33	132	1.48	9.4	9.4
Feb. 1975	12	120	1.03	8.2	8.2
Year:					
1973	91	128.5	1.33	10.6	10.6
1974	81	124.5	1.18	9.4	9.4
1975	88	127.0	1.27	10.2	10.2
Pooled	260	126.7	1.26	10.1	10.1

[1]Includes mature females (≥165 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.

accompanying calves are more likely to be captured and killed in the net because of limitations imposed on endurance of the mother by that of the calf, certainly lower than adult endurance. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples, or, conversely, 2) lactating females were underrepresented. Recent data for *S. attenuata* (J. E. Powers pers. commun.) indicate that small calves are probably overrepresented in small single-set samples of that species. This may be caused by the above-mentioned lesser stamina of calves in the energetically stressful purse seine chase, capture, and release sequence. The lesser year-to-year variation in the estimates yielded by Method 2 also supports the idea that these may be better estimates. If neonates are overrepresented in the samples, however, then the percent pregnant must be underestimated to some unknown, but small, degree. In view of these considerations, both the proportion-in-phase estimate and the cumulative calf length/lactating female estimate are used below as alternatives in estimating pregnancy rate, calving interval, and gross annual reproduction, and we conclude that the true length of lactation in an unperturbed birth-to-weaning period can be assumed to lie somewhere between the estimates yielded by the two methods.

Annual pregnancy rate by Method 1 was calculated by division of the proportion pregnant (Figure 29) by the length of gestation (0.875 yr). The reciprocal of annual pregnancy rate is the esti-

mate of average calving interval. For the Method 2 estimates, calving interval was calculated by summing the phases, taking into consideration overlapping cycles by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant. Lacking an independent estimate of the length of the "resting" phase, the Method 1 estimate for 1973-75 was used as a reasonable approximation in the Method 2 calculations of length of cycle and calving interval.

CHANGES IN REPRODUCTIVE RATES WITH AGE.—Pregnancy rate in the sample decreases with age after about 12 layers (8.0, 11.5, or 10.2 yr, depending upon whether layer Hypothesis I, II, or III is applied, respectively), while lactation rate rises (Figure 30). Assuming that the samples are representative of the population, this may mean that 1) pregnancy rate decreases with age in the individual, or 2) that older females belong to older cohorts in which reproductive rates have been lower than in younger cohorts since recruitment to the breeding population. The former seems most likely; it would appear that older females have fewer calves and nurse them longer. The same result was obtained for *S. attenuata* in the eastern Pacific (Perrin et al. 1976).

Sex Ratios

Sex ratios are at or very near parity at birth and overall in the samples (Table 10), but there were slightly more females than males in adults in the samples for each of the 3 yr 1973–75, a result consistent with that encountered in *S. attenuata* (Perrin et al. 1976) but less pronounced.

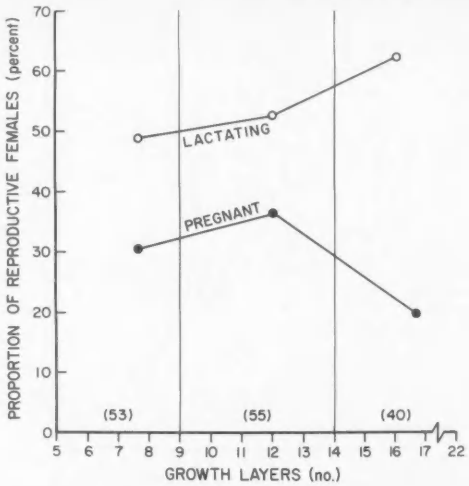

FIGURE 30.—Change in reproductive rates with age in the eastern spinner dolphin. Sample sizes in parentheses.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be made based on 1973–75 samples, the 3 yr for which the samples are large and nonselected with respect to age and sex structures (Table 11). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then the proportion of total females which are reproductive and pregnancy rate (for Method 1) are underestimated and the proportion of total sample female is overestimated, all to an unknown, but probably small, degree. Standard er-

TABLE 10.—Sex ratios in 126 fetuses and 2,261 neonatal-to-adult eastern spinner dolphins. Fetal samples limited to fetuses longer than 15 cm.

Stage	Length (cm)	Sample size (no.)	Average length (cm)	Females		Males		Sex ratio (M ÷ F)
				No.	%	No.	%	
Fetuses	>15	126	49.0	65	51.6	61	48.4	0.94
Neonates to adults	70-129	294	116.0	140	47.6	154	52.4	1.10
	130-149	269	141.2	132	49.1	137	50.9	1.04
	150-159	362	154.9	186	51.4	176	48.6	0.95
	>160 (adult size):							
	1973	408	171.2	207	50.7	201	49.3	0.97
	1974	439	171.3	226	51.5	213	48.5	0.94
	1975	483	172.4	254	52.6	229	47.4	0.90
	1973-75 pooled	1,330	171.7	687	51.7	643	48.3	0.94
	Total:[1]							
	1973	688	—	342	49.7	346	50.3	1.01
	1974	797	—	395	49.6	402	50.4	1.02
	1975	776	—	411	53.0	365	47.0	0.89
	1973-75 pooled	2,261	—	1,148	50.8	1,113	49.2	0.97

[1]Includes six specimens for which length data not available.

TABLE 11.—Calculation of estimates of gross annual reproductive rate of the eastern spinner dolphin, 1973-75. Standard error follows estimate (see text). Sample sizes in parentheses.

Year	*A* Proportion female	*B* Proportion of females reproductive	*C* Annual pregnancy rate		*A* × *B* × *C* Gross annual reproductive rate	
			Method 1	Method 2	Method 1	Method 2
1973	0.497 ±0.019 (690)	0.443 ±0.027 (343)	0.243 ±0.036 (140)	0.450 ±0.042 (140)	0.054 ±0.009 (690)	0.099 ±0.011 (690)
1974	0.496 ±0.018 (797)	0.438 ±0.025 (391)	0.444 ±0.040 (158)	0.474 ±0.042 (158)	0.096 ±0.010 (797)	0.103 ±0.011 (797)
1975	0.530 ±0.018 (776)	0.432 ±0.024 (410)	0.380 ±0.040 (149)	0.459 ±0.041 (149)	0.087 ±0.010 (776)	0.105 ±0.011 (776)
1973-75 pooled	0.508 ±0.011 (2,262)	0.437 ±0.015 (1,144)	0.360 ±0.028 (447)	0.461 ±0.024 (447)	0.080 ±0.006 (2,262)	0.102 ±0.006 (2,262)

rors (SE) are attached to the various estimates where sample size ≥100, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of SE as:

$$SE = \sqrt{p(1-p)/n}.$$

Although gross annual reproductive rate as calculated in Table 11 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), allowing estimation of the variance by the above method. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The only statistically significant differences among the estimates year-to-year (at $\alpha = 0.05$) are between the Method 1 estimates for 1973 and 1974 of annual pregnancy rate and, as a result of that, gross annual reproductive rate. This sharp and real shift cannot be accounted for by a time-sampling effect, because seasonal coverage in the 2 yr was approximately the same. Prompted by the knowledge that areal variation may exist in the timing of calving peaks and/or in the degree of breeding synchrony (see Length of Gestation and Fetal Growth), we divided the data for each of the years into three geographical strata: an "inside" sample, an "outside" sample, and a "southern sample" (Figure 31). More of the 1973 sample was taken from the outside area than from the inside area (108 versus 28), and the reverse was true in 1974 (46 versus 106). The southern samples, 5 in 1973 and 14 in 1974, were too small for analysis. Comparison of the distribution of reproductive condition in inside and outside samples in 1973 and 1974, however, reveals very small areal differences compared with those between years (Table 12). It must be concluded that the sharp increase in percent pregnant and decrease in percent lactating from 1973 to 1974 is not a seasonal or areal effect. Several other possible explanations exist, to wit:

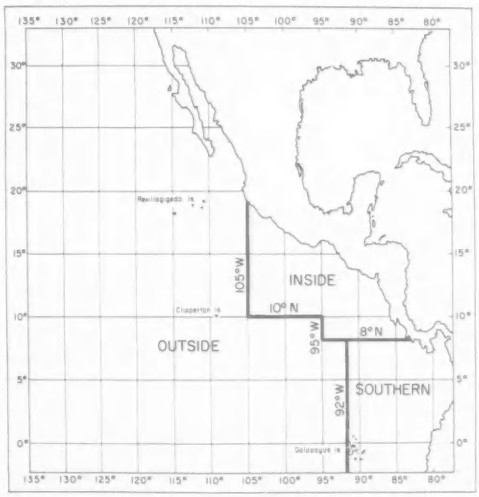

FIGURE 31.—Areas used to stratify 1973-74 samples of distribution of reproductive condition in female eastern spinner dolphins.

TABLE 12.—Distribution of reproductive condition in area-stratified samples of sexually adult female eastern spinner dolphins in 1973 and 1974.

Year	Inside (*n* = 134)	Outside (*n* = 154)
	(*n* = 28)	(*n* = 108)
1973	14.3% pregnant	19.4% pregnant
	57.1% lactating	61.1% lactating
(*n* = 136)	3.6% pregnant and lactating	0.0% pregnant and lactating
	25.0% "resting"	18.5% "resting"
	0.0% postreproductive	0.9% postreproductive
	(*n* = 106)	(*n* = 46)
1974	38.7% pregnant	39.1% pregnant
	48.1% lactating	50.0% lactating
(*n* = 152)	0.0% pregnant and lactating	4.3% pregnant and lactating
	10.4% resting	6.5% resting
	2.8% postreproductive	0.0% postreproductive

1) The samples were biased with respect to reproductive structure of the population, in one or both years or differently in the 2 yr.
2) The change was a real and normal event, perhaps reflecting differential breeding rates in single-year cohorts (the data suggest about a 3-yr cycle—see below—and the 1974 rates were similar to those for 1971).
3) An anomalous increase in pregnancy rate occurred from 1973 to 1974, perhaps related to exploitation in the tuna fishery or to natural variation in the pelagic environment.

The balance of evidence discussed above favors the first alternative, suggesting that the Method 2 estimates of gross annual reproduction are the more accurate of the two alternative sets of estimates.

DISCUSSION

Comparison with the Spotted Dolphin

The estimated gross reproductive rates (Method 1) for the eastern spinner dolphin are lower than those estimated for the offshore spotted dolphin by Perrin et al. (1976), 10 to 11%, as opposed to 14%. Three major points of difference between the data for the two species contribute to this disparity.

1) A higher proportion of the spotted dolphins were females (55.1% as opposed to 50.8% in the present 1973–75 sample of eastern spinner dolphins).
2) The proportion of total females which were reproductive was higher for the spotted dolphin (55.7% as opposed to 43.7% for the eastern spinner dolphin).
3) There is apparently much less overlapping of reproductive cycles in the eastern spinner dolphin than in the spotted dolphin in the eastern Pacific. Only 1.4% of lactating females examined were simultaneously pregnant, as opposed to 9.6% in the spotted dolphin, a sevenfold difference. At least part of this difference may be inherent in the species; the rate in the unexploited western Pacific population of spotted dolphin is 5.1% (Kasuya et al. 1974), still nearly four times greater than in the eastern spinner dolphin.

In summary, the data suggest that there is an inherent difference in reproductive capability between the spotted and spinner dolphins, but that part of the total difference in present reproductive rate may be related to differential exploitation. Gross annual reproductive rate in the unexploited western Pacific population of *S. attenuata* is estimated at 0.094 (calculated from data in Kasuya et al. 1974—0.57 female × 0.61 mature × 0.27 annual pregnancy rate = 0.094/yr), as opposed to 0.144 in the exploited eastern Pacific population of the same species, a possible example of difference in rate correlated with differential exploitation. Whereas the western Pacific population is thought to be virtually unexploited and at its original size, the eastern Pacific population is estimated to be at 62% of its original, preexploitation size (midpoint estimate).[8]

Comparison with Other Cetaceans

The estimates of gross annual reproductive rate for the eastern spinner dolphin lie at the lower end

[8]Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. SWFC Admin. Rep. LJ-76-29, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 109 p. (Unpubl. rep.)

TABLE 13.—Estimated gross annual reproductive rate of the eastern spinner dolphin compared with estimated rates for other cetaceans. Data for *S. attenuata* from Perrin et al. (1976) for eastern Pacific and Kasuya et al. (1974) for western Pacific; for *S. coeruleoalba* from Kasuya (1972), for *Delphinus* from Danilevskiy and Tyutyunnikov (1968); for *Globicephala* from Sergeant (1962); for *Delphinapterus* from Sergeant (1973); and for *Eschrichtius* from Rice and Wolman (1971). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975); alternative common name in parentheses.

Species and locality	Exploited (now or in past)	Gross annual reproductive rate
Eastern spinner dolphin (porpoise), *Stenella longirostris* subsp.	Yes	0.08 (pooled 1973-75)
Spotted dolphin (porpoise), *S. attenuata*		
Eastern Pacific	Yes	0.14
Western Pacific	No	0.09
Striped dolphin (streaker porpoise), *S. coeruleoalba*, in western Pacific	Yes	0.11
Common dolphin (whitebelly porpoise), *Delphinus delphis*, in Black Sea	Yes	0.14
Long-finned pilot whale (pothead whale), *Globicephala melaena*, in western North Atlantic	Yes	0.10 to 0.13
White whale (beluga), *Delphinapterus leucas*, in western Hudson Bay	Yes	0.12
Gray whale, *Eschrichtius robustus*, in eastern North Pacific	Yes	0.13

of the range of estimates for other cetaceans (Table 13), with only the estimate for 1974 included in the range. The estimated rates for populations thought to have declined due to exploitation (*S. attenuata* in the eastern Pacific—Perrin et al. 1976; *D. delphis* in the Black Sea—Danilevskiy and Tyutyunnikov 1968; and *Eschrichtius*—Rice and Wolman 1971) are very close to each other, at 13 or 14%.

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PRODUCTION BY THREE POPULATIONS OF WILD BROOK TROUT WITH EMPHASIS ON INFLUENCE OF RECRUITMENT RATES

ROBERT F. CARLINE[1]

ABSTRACT

Populations of wild brook trout, *Salvelinus fontinalis*, in three small ponds in northern Wisconsin were studied for 4 yr to determine annual production with particular emphasis on influence of recruitment rates. Recruitment included trout hatched in ponds and immigrants from adjacent waters. Age-specific growth rates and densities of trout were estimated in spring and fall. Harvest of trout was estimated through partial creel surveys.

Among populations annual production ranged from 26 to 331 kg/ha and was directly related to recruitment rates. Production was most influenced by population biomass. Instantaneous growth rates did not vary significantly within or among populations despite large differences in population densities; hence, variations in production appeared unrelated to growth rates. Among populations, yield of trout ranged from 25 to 72 kg/ha and fishing pressure ranged from 154 to 1,405 h/ha. Proportion of annual production that was harvested was directly related to fishing pressure.

Production of fry during the first 9 mo of life may have been overestimated because mortality rates from emergence to fall were assumed constant. Estimates of production of adult trout could have been positively or negatively biased depending upon immigration patterns. Despite these possible errors, it was clear that recruitment was the most important factor affecting production.

Estimation of fish production has gained widespread acceptance because it provides some measure of a system's capacity to support species of interest (Gerking 1967). Production is defined as the total elaboration of tissue by a population during a specified time interval, regardless of the fate of that tissue (Ivlev 1945). Unlike standing crop estimates, production is a dynamic population parameter that is useful in evaluating the environmental performance of a fish population (Le Cren 1972). Studies by Ricker and Foerster (1948), Allen (1951), and Hunt (1971) are good examples of how fish production has been related to predation, the food supply, and habitat suitability. While many studies have considered the effects of standing crops, growth rates, and mortality on production, the importance of recruitment has not been well defined.

In northern Wisconsin, standing crops of wild brook trout, *Salvelinus fontinalis*, in spring-fed ponds vary greatly. Some ponds have filled-in naturally and living space is limiting. In others, living space appears to be adequate, but spawning areas are small or nonexistent and recruitment seems to be limiting standing crops of trout. The objective of this study was to determine annual production by three populations of wild brook trout with particular emphasis on the influence of recruitment rates. Recruitment includes all trout hatched in the ponds plus all immigrant trout.

The ponds were chosen because they differed greatly in areas available for spawning and numbers of immigrating trout. Ponds were similar in size and watershed characteristics, and springs were the primary sources of water. Outlet streams, which flowed into larger streams and/or lakes, provided convenient sampling boundaries, but did not impede movement of trout into or out of the ponds. I estimated densities and growth rates of trout every spring and fall from 1968-72 and conducted partial creel surveys during 3 yr of the study to estimate trout yields.

DESCRIPTION OF STUDY AREA

The study ponds, situated in a terminal moraine, are located within 7 km of each other in Langlade County, north central Wisconsin. The moraine is composed of glacial till ranging in size from sand to large boulders. These permeable

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materials permit a relatively uninhibited flow of ground water that is the main source of water for all ponds. Hoglot and Clubhouse springs are on state-owned land and Maxwell Springs is privately owned. The ponds are located in wooded lowlands and all three drain into trout streams that are part of the Wolf River drainage, a major Lake Michigan watershed.

The ponds are similar in size and have relatively short exchange times due to large inflows of ground water (Table 1). Because all ponds are supplied by the same aquifer, concentrations of common ions are similar. Bottom materials consist mostly of marl and organic matter. About 10% of the shorelines in Maxwell and Hoglot springs are composed of gravel with emerging ground water and brook trout spawn in these areas. Numbers of trout redds in Hoglot Springs ranged from 85 to 105/ha of pond area, and in Maxwell Springs redd densities ranged from 165 to 230/ha. Clubhouse Springs lacks gravel areas with upwelling ground water and brook trout do not spawn there.

Continual inflow of ground water and rapid exchange times tend to moderate pond temperatures and maintain relatively high concentrations of dissolved oxygen. Ground water temperatures typically range from 6° to 7°C and concentrations of dissolved oxygen, from 8 to 9 ppm. Pond temperatures in summer at depths of 15 cm rarely exceed 16°C. Concentrations of dissolved oxygen rarely fall below 5 ppm at any depth throughout the year and they usually exceed 7 ppm. Ponds are ice-covered from early November to late March.

All ponds supported dense beds of aquatic vegetation. *Chara vulgaris* covered about 40% of the bottom in Clubhouse Springs and 15% in Hoglot Springs. *Anacharis canadensis*, the only common plant in Maxwell Springs, extended over 50% of the bottom.

Fish communities in the three ponds were similar. Brook trout composed the major portion of fish biomass. A small population of brown trout, *Salmo trutta*, in Clubhouse Springs never accounted for more than 10% of the total number of trout. The white sucker, *Catostomus commersoni*; mottled sculpin, *Cottus bairdi*; Central mudminnow, *Umbra limi*; and brook stickleback, *Culaea inconstans*, were common in all ponds. The brook stickleback was an important food source for age 3 and older trout; however, benthic invertebrates composed the major portion of the diet for trout of all sizes.

TABLE 1.—Some physicochemical features of study ponds in north central Wisconsin. Chemical measurements were taken in April 1970.

Item	Clubhouse Springs	Hoglot Springs	Maxwell Springs
Surface area (ha)	0.81	0.38	0.97
Mean depth (m)	1.11	0.64	0.86
Outlet discharge[1] (m^3/s)	0.03	0.005	0.05
Exchange time[2] (days)	3.3	5.6	2.0
Specific conductance (μmho/cm)	341	335	310
Total alkalinity (mg/l as $CaCO_3$)	180	153	168
Calcium (mg/l)	42	40	39
Nitrate (mg/l-N)	0.5	0.7	1.1
Dissolved phosphorus (mg/l-P)	0.02	0.01	0.03

[1]Summer base flow.
[2]Pond volume/discharge.

METHODS

Trout populations were estimated in spring and fall using Bailey's modification of the Petersen mark and recapture method (Ricker 1975). Trout were captured at night with electrofishing gear and held overnight in screen cages. The following day, fish were anesthetized, measured to the nearest 2 mm (total length), weighed to the nearest gram, given a temporary mark by clipping the tip of the caudal fin, and released. A second electrofishing run was made two or more days later. Proportions of marked trout captured during the second electrofishing sample were used to calculate confidence limits for population estimates (Adams 1951).

Age structures of trout populations were determined from length distributions of known age fish and scale analyses. Fall fingerlings and spring yearlings, determined from length-frequency distributions, were permanently marked by fin removal. Estimated numbers of trout in each 25-mm length group were placed in appropriate age-groups based on relative proportions of known age fish. The electrofishing gear was size selective. Efficiency was lowest for smallest fish and increased until fish size reached about 12 cm. Separate estimates for 25-mm length intervals avoided bias due to size selectivity of electrofishing gear.

Maxwell outlet and Elton Creek, the stream into which Clubhouse Springs flowed, were sampled with electrofishing gear to obtain data on growth rates of trout in outlet waters and on movement of trout between ponds and adjoining streams. A 1-km section of Elton Creek was sampled five times from 1968 to 1971; Clubhouse

outlet joined this section at its midpoint. Maxwell outlet (200 m) was sampled in 1969 and 1972. All trout were measured, about 25% were weighed, and fall fingerlings and spring yearlings were permanently marked by fin removal.

Sampling dates in ponds varied from year to year. I estimated mean lengths and weights of each cohort on 15 April and 15 September so that growth rates from different years could be compared. Mean weights of individuals in each year class were determined graphically by assuming constant instantaneous rates of growth. By graphically estimating mean length, I assumed length increased linearly between successive estimates. Most of the adjustments in length or weight involved extrapolating over periods <2 wk and size changes were usually <5%.

Year class biomass was estimated by multiplying mean weights of individual trout by year class density. Biomasses in spring and fall were averaged to calculate mean biomass ($\bar{B}$). I followed procedures suggested by Ricker (1975) to calculate instantaneous rates of growth by weight (G), total mortality (Z), natural mortality (M), and fishing mortality (F). Production, the product of G and $\bar{B}$, was computed semiannually for each cohort. Production by fingerling trout was calculated from emergence (1 March) to time of spring population estimate and from spring to fall. A mean weight of 0.04 g was assigned to emergent fry (Hunt 1966). I assumed that instantaneous growth and mortality rates from emergence to fall were constant. Mean annual biomass of each cohort was calculated by weighting mean biomasses in the two intervals according to interval lengths. Annual production was calculated by summing production during the two intervals and expressing the sum for 365-day periods.

Potential egg production for each population was estimated from numbers of mature females in fall and from a relationship between total length of females and number of eggs. Fecundity of trout was determined from 83 females that were collected from two ponds in the same watershed as the study ponds. Trout were collected in early October, about 2 wk prior to spawning. Mature ova could be easily distinguished from recruitment eggs on the basis of size and color (Vladykov 1956). Data on trout length, weight, and total number of eggs were fitted to linear, curvilinear, and logarithmic regression models. A linear regression of total trout length and number of eggs yielded the highest correlation coefficient.

At Clubhouse and Hoglot springs, densities of some year classes increased during sampling intervals because of immigration from outlets or adjoining streams. Numbers of immigrants were estimated by first calculating expected densities at the end of sampling intervals by using mean, age-specific mortality rates; expected densities were then subtracted from actual densities. If the expected number of trout at the end of an interval was within 10% of the actual number or the difference was negative (suggesting emigration), it was assumed no immigration had occurred. Age-specific mortality rates for trout in Clubhouse and Hoglot springs were estimated from permanently marked fish. For some age groups, mortality rates could not be estimated because of insufficient numbers of marked fish. In these instances I used age-specific mortality rates of the population in Maxwell Springs, where immigration did not influence year class densities (discussed later).

Harvest of trout from Clubhouse and Hoglot springs was estimated from partial creel surveys in 1969, 1970, and 1972. State-wide angling regulations included a bag limit of 10 trout/day and minimum length of 154 mm (6 in). Census clerks worked five randomly chosen days per week during the entire fishing season, mid-May to mid-September. Catch rates were estimated from data collected during interviews of anglers, and fishing pressure was calculated from instantaneous counts of anglers (Lambou 1961). Harvest was estimated monthly from the product of the hours of fishing and numbers of trout caught per hour. Harvested trout were measured, examined for permanent marks, and scales were collected from a sample of the catch. Harvest data from Maxwell Springs were compiled by the owner and others who fished the pond. Ages of harvested trout from Clubhouse and Hoglot springs were determined from scales and size distributions of permanently marked fish. Ages of trout harvested from Maxwell Springs were estimated from comparisons of lengths of harvested trout with lengths of known age fish in spring and fall.

RESULTS

Population Densities and Biomass

Electrofishing was the most efficient method of collecting trout in these shallow ponds. Population estimates derived from collections with trap

nets and seines showed that collecting trout with just electrofishing gear did not yield biased estimates (Carline unpubl. data). Efficiency of the electrofishing gear usually increased with trout size (Table 2). Mean proportions of marked trout captured during the second electrofishing sample for age 0 to 3 fish were 0.18, 0.31, 0.35, and 0.39, respectively. Recapture efficiencies were always lowest for age 0 trout and values ranged from 0.05 to 0.30. For age 1 and older fish, precision of estimates depended mostly upon sample size and confidence limits for the oldest age groups were generally broad because of their low densities (Table 2).

TABLE 2.—Examples of trout population estimates and 95% confidence limits by age-groups. Data were collected in fall 1970.

Item	0	1	2	3	4
Clubhouse Springs:					
Mean length (mm)	99	175	211	274	
Proportion of marked fish recaptured	0.30	0.40	0.41	0.50	
Population estimate (no./ha)	386	363	84	6	
95% confidence limits	234	279	47	0	
	782	466	124	40	
Maxwell Springs:					
Mean length (mm)	92	147	182	220	287
Proportion of marked fish recaptured	0.05	0.43	0.53	0.34	0.22
Population estimate (no./ha)	2,195	1,572	909	433	28
95% confidence limits	1,183	1,408	845	367	17
	3,944	1,778	1,003	507	56

Clubhouse Springs

The brook trout population in Clubhouse Springs was the smallest of the three populations. Because no spawning areas were present, this population was entirely dependent upon immigration from downstream areas. Trout densities usually declined from spring to fall and only age 0 trout appeared to immigrate in substantial numbers oversummer (Figure 1). Total trout numbers in 3 of 4 yr increased overwinter due to immigration. Numbers of trout in spring ranged from 390 to 1,750/ha and densities in fall ranged from 390 to 840/ha. Age structure of the population was at times atypical because young age groups were less numerous than older ones, owing to differential rates of immigration.

Changes in population biomass closely paralleled numerical changes. Biomass in spring averaged 45 kg/ha and in fall 26 kg/ha (Table 3). In all years, population biomass increased from fall to spring, the period when immigration appeared greatest.

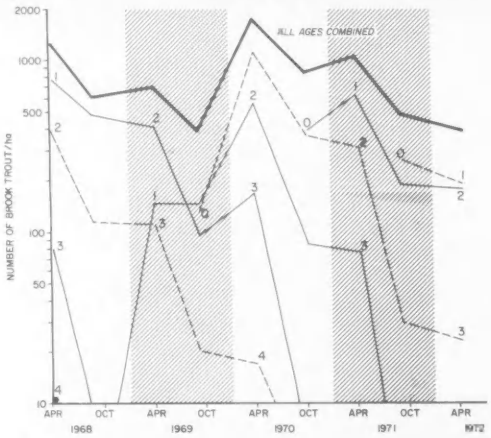

FIGURE 1.—Estimated numbers of brook trout in Clubhouse Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

TABLE 3.—Estimated biomass (kilograms per hectare) by age-group of brook trout in study ponds, 1968-72. Mean weights of individuals in each age-group were multiplied by estimated density of the age-group to calculate biomass.

Site and date	0	1	2	3	4	5	Total
Clubhouse Springs:							
27 Mar. 1968		10.9	15.6	8.7	3.5		38.7
28 Aug. 1968		22.9	10.8	1.2	1.7		36.6
8 Apr. 1969		3.0	23.7	14.4	5.2		46.3
8 Sept. 1969	1.8	7.6	10.4	4.3	0.4		24.5
1 Apr. 1970		17.2	26.2	20.4	4.6		68.4
8 Sept. 1970	3.5	17.4	7.0	1.2			29.1
29 Apr. 1971		12.0	22.9	12.2	2.3		49.4
8 Sept. 1971	2.1	6.6	3.1	0.2			12.0
21 Apr. 1972		3.0	13.1	4.4	0.7		21.2
Hoglot Springs:							
2 Apr. 1968		22.6	69.1	26.5	11.2		129.4
26 Aug. 1968	6.8	26.1	35.8	13.6	3.6		85.9
8 Apr. 1969		5.0	37.2	66.8	8.1		117.1
8 Sept. 1969	15.9	33.7	47.6	12.5	2.3		112.0
13 Apr. 1970		13.0	38.3	38.5	13.3		103.1
8 Oct. 1970	16.9	91.0	36.4	9.1	0.7		154.1
28 Apr. 1971		10.8	70.7	21.5	2.1		105.1
21 Sept. 1971	7.0	26.6	40.7	5.6	0.2		80.1
2 May 1972		10.8	17.0	6.5	2.5		36.8
Maxwell Springs:							
9 Apr. 1969		34.4	50.8	26.3	41.6	80.3	233.4
13 Oct. 1969	27.0	55.8	88.8	29.3	20.8	16.1	237.8
26 Mar. 1970		25.3	47.3	69.6	16.2	12.4	170.8
6 Oct. 1970	22.0	56.6	63.6	53.7	6.9	2.6	205.4
26 Apr. 1971		8.2	48.0	46.9	17.6	0.5	121.2
20 Sept. 1971	24.6	19.2	32.6	13.8	0.9		91.1
26 Apr. 1972		27.1	7.3	7.1	3.7		45.2
29 Sept. 1972	14.8	46.6	11.0	4.5	1.4		78.3

Hoglot Springs

Although some fingerlings were hatched in Hoglot Springs, numbers of immigrating trout, particularly age 1 fish, had the most impact on population size. In 3 of 4 yr, densities of yearling trout increased oversummer, and during the

winter of 1968-69 fall 2-yr-olds increased by 50% (Figure 2). Mean population densities were higher in fall than in spring (4,480 vs. 3,200/ha) because of recruitment by age 0 trout and age 1 trout.

Trout migrating into Hoglot Springs had a marked effect on population biomass. Biomass was highest in fall 1970 because of the large stock of yearlings (91 kg/ha), most of which were recent immigrants (Table 3). Little immigration occurred oversummer in 1971 and overwinter in 1971-72. As a result, population biomass in spring 1972 reached its lowest level of the 4-yr period.

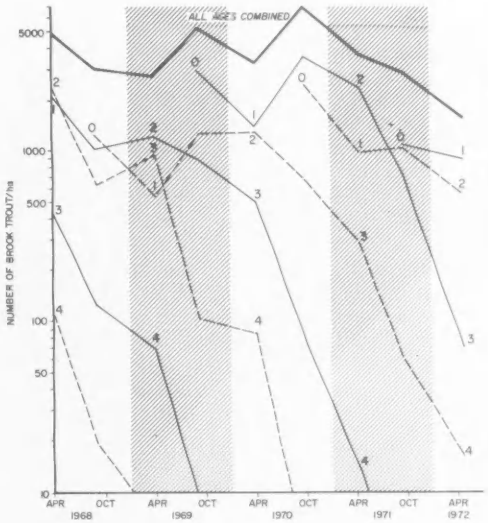

FIGURE 2.—Estimated numbers of brook trout in Hoglot Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

Maxwell Springs

Except for 1972, Maxwell Springs supported the largest of the three populations, and natural reproduction accounted for nearly all recruitment. Two experiments were conducted to evaluate the extent of immigration from Maxwell outlet into the pond. In June 1969 and April 1972, a total of 602 ages 0 and 1 trout were captured in the outlet and marked. In subsequent surveys of the pond, I examined over 4,000 trout, only 3 of which had been marked in the outlet. Hence, I concluded that trout reared in the outlet did not materially affect recruitment in the pond.

From April 1969 to September 1972 trout densities in Maxwell Springs declined markedly (Figure 3). Spring densities steadily decreased from 7,300/ha in 1969 to 1,810/ha in 1972. Fall populations followed a similar trend. This decline was due in part to decreasing numbers of fall fingerlings. Densities of age 0 trout ranged from 4,085/ha in October 1969 to 1,940/ha in September 1972. However, even the 1969 year class, which was larger than the succeeding three year classes, had to be smaller than the 1968 and 1967 year classes, based on their densities as ages 1 and 2 fish in April 1969 (Figure 3). I estimated numbers of fall fingerling for the 1967 and 1968 year classes by using average mortality rates of succeeding year classes. The 1967 year class was estimated at 16,000/ha and the 1968 year class at 8,300/ha. Thus, numbers of fall fingerlings had steadily declined from 1967 to 1972 with one exception, the 1971 year class.

The reduction in year class strength in Maxwell Springs may have been related to the installation of a weir in the pond outlet in 1968. The weir, which was used to monitor discharge, was located 132 m downstream from the pond and it created

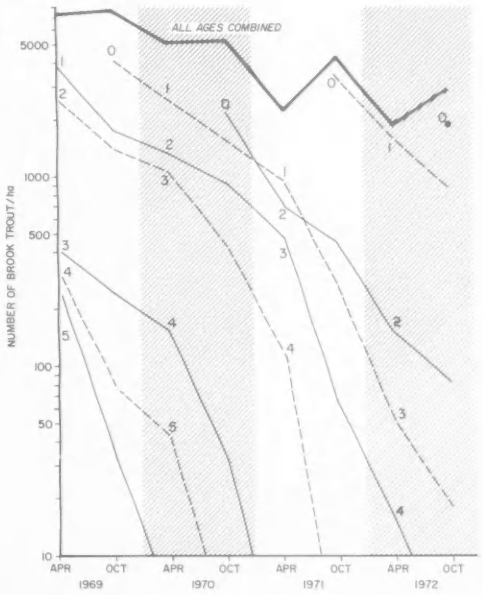

FIGURE 3.—Estimated numbers of brook trout in Maxwell Springs, 1969-72. Numbers designate age-groups and hatched areas separate calendar years.

an impoundment that extended to within 5 m of the pond. The impounded area was heavily silted by fall 1968 and I counted only four redds there. The owner had reported that large numbers of brook trout spawned in this area prior to weir installation. In fall 1974, 1 yr after the weir had been removed, I counted 34 redds and about half the streambed was covered with silt. Since effects of impoundment were still evident, this portion of the outlet may have provided much more spawning area than was evident in 1974. Possibly, immigration was an important source of recruitment prior to this study.

Population declines at Maxwell Springs were accompanied by changes in age structure. In April 1969, density of age 3 and older trout was nearly 1,000/ha and they totaled 233 kg/ha, or 63% of population biomass (Table 3). By September 1972, density of age 3 and older trout was 22/ha and biomass was about 6 kg/ha, the lowest in the 4-yr period.

Mortality

Numbers of fall fingerlings in Hoglot and Maxwell springs represented from 0.2 to 1% of the estimated number of eggs deposited the previous fall. I sampled 52 redds in five different ponds to assess preemergence mortality. Numbers of eggs per redd ranged from about 30 to 220. Percentage of live embryos in individual redds ranged from 76 to 99 (mean = 89%); stage of development of these embryos varied from eyed egg to alevin. Due to additional mortality to emergence, I used 80% of potential egg deposition to estimate numbers of emerging fry. Although highest mortality rates in both ponds occurred during years of highest egg production, egg production and fingerling mortality were not significantly correlated (Table 4).

To estimate age-specific total mortality rates of trout in Maxwell Springs, I assumed that immigration was negligible. At Clubhouse and Hoglot springs, where immigration was substantial, unmarked residents and immigrants could not be separated; therefore, mortality rates were calculated using only permanently marked trout. Numbers of age 2 and older trout were usually too small to allow estimation of mortality rates.

Mean rates of oversummer mortality in Maxwell and Hoglot springs increased with age (Table 5). Overwinter mortality rates at Maxwell Springs also increased with age, except that age 0 trout had higher mean mortality rates than did age 1 trout. However, within years there was considerable variability between age of fish and mortality rates. In all ponds mean mortality rates oversummer exceeded overwinter rates.

TABLE 4.—Estimated egg production of brook trout populations and densities of fall fingerlings. Egg deposition was estimated from number of mature female trout in fall and the relationship of fecundity (Y) and trout length in millimeters (X); $Y = -588 + 6.14X$. Instantaneous mortality rates (Z) were based on 80% of egg production and were corrected for 182-day intervals.

Pond	Year class	No. eggs/ha	No. fall fingerlings/ha	Z/182 days
Hoglot Springs	1969	281,000	2,938	4.111
	1970	276,000	2,481	3.681
	1971	433,000	1,049	5.148
	Mean	330,000	2,156	4.313
Maxwell Springs	1969	543,000	4,085	3.742
	1970	550,000	2,195	4.384
	1971	739,000	3,519	4.549
	1972	212,000	1,945	3.800
	Mean	511,000	2,936	4.119

Immigration

Estimation of immigration rates at Clubhouse and Hoglot springs were based on mortality rates calculated from relatively small numbers of permanently marked trout and from mean, age-specific mortality rates of trout from Maxwell Springs (Table 5). Although accuracy of these estimates is suspect, they should be useful in illustrating seasonal differences in immigration and in assessing the effect of immigration on recruitment.

At Clubhouse Springs most immigration occurred overwinter and age 0 trout made up 55% of all migrants (Table 6). Largest migrations into Hoglot Springs occurred between April and September when age 1 trout accounted for 73% of all migrants. In both populations periods of peak immigration coincided with highest population densities. Immigration was the only source of recruitment at Clubhouse Springs; at any one time more than half the population consisted of fish that had immigrated within the previous 6 mo. At Hoglot Springs percentages of recent immigrants ranged from 8.2 to 54.9 (mean = 34%).

If estimates of trout migrating into Hoglot Springs are reasonable, immigration accounted for a major portion of total recruitment. The four year classes produced in the pond from 1968 to 1971 amounted to 7,700 fall fingerlings/ha. About 3,800 of these fish survived to the following spring.

TABLE 5.—Instantaneous total mortality rates for 182-day intervals. Mortality rates of trout in Maxwell Springs were calculated from year class densities. Mortality rates of trout in Hoglot and Clubhouse springs were calculated from permanently marked fish. Estimated numbers of trout at the end of sampling intervals given in parentheses.

Interval and year	Maxwell Springs					Hoglot Springs		Clubhouse Springs
	[1]0	1	2	3	4	1	2	1
Oversummer:								
1968						2.254		1.238
						(72)		(75)
1969		0.766	0.573	0.510	1.521	0.408	2.151	1.914
		(1,691)	(1,368)	(233)	(109)	(110)	(7)	(13)
1970		0.448	0.373	0.850	1.492	0.725	1.080	1.489
		(1,525)	(882)	(420)	(31)	(158)	(8)	(81)
1971		0.500	1.552	2.439	4.404	1.382	1.631	1.522
		(442)	(264)	(62)	(3)	(33)	(20)	(65)
1972		0.681	0.670	1.185	1.532			
		(863)	(82)	(17)	(4)			
Mean		0.599	0.792	1.246	2.237	1.192	1.742	1.541
Overwinter:								
1968-69						0.175		0.804
						(58)		(28)
1969-70	0.530	0.282	0.306	0.826	1.085	1.312		1.662
	(2,457)	(1,310)	(1,039)	(110)	(41)	(23)		(2)
1970-71	1.048	0.444	0.606	1.243	2.498	0.687		0.573
	(664)	(931)	(450)	(106)	(2)	(74)		(39)
1971-72	0.659	0.917	1.398	1.211	0.926	0.826		1.186
	(1,549)	(147)	(49)	(14)	(1)	(12)		(15)
Mean	0.746	0.548	0.770	1.093	1.503	0.750		1.056

[1]Age at start of interval.

TABLE 6.—Estimated numbers of immigrant brook trout present by age-groups at the end of sampling intervals. Summer intervals were from April to September and winter intervals from September to the following April. Percent of population at the end of the interval composed of recently immigrated trout given in parentheses.

Year and interval	Clubhouse Springs					Hoglot Springs				
	0	1	2	3	Sum	0	1	2	3	Sum
1968										
Summer	0	346	0	0	346 (57)		207	42	0	249 (8)
Winter	147	277	65	14	503 (74)	0	802	659	34	1,495 (55)
1969										
Summer	130	104	0	0	234 (60)		1,046	619	0	1,665 (32)
Winter	955	514	130	12	1,611 (92)	191	767	149	56	1,163 (36)
1970										
Summer	387	102	0	0	489 (58)		3,205	417	0	3,622 (53)
Winter	451	215	46	6	718 (70)	0	773	0	0	773 (21)
1971										
Summer	262	0	0	0	262 (55)		645	133	0	778 (27)
Winter	86	128	12	0	226 (57)	478	157	0	0	635 (41)
Sum	2,418	1,686	253	32	4,389	669	7,602	2,019	90	10,380
Percent	55.1	38.4	5.8	0.7		6.4	73.2	19.5	0.9	

During this 4-yr period over 9,700 age 1 and older trout immigrated into the pond, hence, migrants accounted for about 70% of total recruitment of yearling and older trout.

It is likely that trout migrating from Elton Creek into Clubhouse Springs were smaller than pond residents because: 1) trout in Elton Creek grew more slowly than those in Clubhouse Springs and 2) permanently marked trout in the pond, i.e. residents, were larger than unmarked trout, which were mostly recent immigrants. From 1968 to 1970 fall fingerlings in Elton Creek averaged 4.2 g and those in Clubhouse Springs were 9.6 g. Fall yearlings in Elton Creek averaged 30 g and yearlings in the pond were 46 g. In spring and fall, marked yearlings in Clubhouse Springs were about 20% heavier than unmarked yearlings. For age 2 trout in spring, marked trout were 58% larger than unmarked ones. I made similar comparisons for ages 1 and 2 trout in Hoglot Springs; differences in sizes among marked and unmarked trout were not consistent and I concluded that migrants were similar in size to pond residents.

Growth

Among populations, mean size attained by trout of a given age was greatest in Clubhouse Springs (Table 7). After the first full year of life trout in

TABLE 7.—Estimated mean annual lengths (millimeters) and weights (grams) of brook trout on 15 April and 15 September. Data from Clubhouse and Hoglot springs were from 1968-71 and those from Maxwell Springs were from 1969-72.

Pond and month	Age 0		1		2		3		4	
	L	W	L	W	L	W	L	W	L	W
Clubhouse Springs:										
April			126	19	176	55	229	127		
September	105	13	166	49	212	105	276	238		
Hoglot Springs:										
April			107	10	150	31	199	72	241	136
September	58	6	130	26	178	56	226	118		
Maxwell Springs:										
April			106	12	154	38	203	89	264	172
September	89	7	147	34	200	88	246	168	300	284

Clubhouse Springs were from 58 to 90% larger than spring yearlings in Hoglot or Maxwell springs. Although trout in Clubhouse Springs maintained a size advantage over their counterparts in the other ponds after the first growing season, age-specific instantaneous growth rates for all populations were similar. I compared mean age-specific growth rates for intervals of April to September and September to April for ages 1-3 trout. There were no significant differences for similar age trout among populations (t-test $P>0.05$). During summer instantaneous growth rates of trout tended to be highest in Maxwell Springs, but there were no consistent differences during winter intervals.

Growth rates of fingerling trout were inversely related to their density (number or weight) when data from all populations were combined (Table 8). Density of yearling trout also had an effect on growth of fingerlings; correlation coefficients were highest when fingerling growth was related to combined density of fingerlings and yearlings. Effects of density on growth rates of age 1 and older trout were inconsistent. When instantaneous growth rates were used as the dependent variable and density in numbers or weight was the independent variable, correlation coefficients were consistently low (Table 8). When age-specific growth was expressed as mean weight or length in September or weight gain from April to September, correlation coefficients were consistently high (Figure 4). The lack of correlation between instantaneous growth rates and density may have been due to underestimation of mean weights of trout in fall, particularly in Clubhouse Springs. Biases could have resulted from: 1) immigration of trout smaller than pond residents, 2) differential exploitation of faster growing individuals in a year class, and 3) errors in estimating year class densities. The lack of correspondence between instantaneous growth rates and other growth parameters has been noted in other studies (Eipper 1964).

Harvest

Fishing success and harvest of trout were influenced by trout densities and fishing pressure. Maxwell Springs supported the largest trout population in 1969 and 1970 and catch rates were highest (Table 9). Among populations annual catch rates were positively related to spring densities of age 1 and older trout ($r = 0.88$; $P<0.01$). There was a significant correlation between biomass of trout harvested (yield) and the

TABLE 8.—Linear correlation coefficients for growth and density of trout ages 0 to 3 in study ponds. (df = 10; $*P<0.05$, $**P<0.01$.)

Independent variable	Age-group of dependent variable	Instantaneous growth rates	Mean length on 15 Sept.	Mean weight on 15 Sept.	Weight gain Apr.-Sept.
Mean trout biomass (kg/ha) of:					
Age 0	0	−0.62*	−0.59		
Age 1		−0.86**	−0.72*		
Ages 0 and 1		−0.85**	−0.76**		
Age 1	1	−0.08	−0.38	−0.61*	−0.53
All ages		0.13	−0.66*	−0.72**	−0.59*
Age 2	2	0.04	−0.81**	−0.79**	−0.62*
All ages		0.14	−0.72**	−0.68*	−0.48
Age 3	3	−0.05	−0.68*	−0.64*	−0.58*
All ages		−0.07	−0.82**	−0.79**	−0.68*
Mean trout density (no./ha) of:					
Age 0	0	−0.78*	−0.84**		
Age 1		−0.67*	−0.64*		
Ages 0 and 1		−0.82**	−0.85**		
Age 1	1	0.01	−0.57	−0.70*	−0.62
All ages		0.01	−0.66*	−0.77**	−0.63*
Age 2	2	0.06	−0.87**	−0.86**	−0.68*
All ages		0.17	−0.71**	−0.69*	−0.46
Age 3	3	−0.09	−0.82**	−0.76**	−0.67*
All ages		−0.12	−0.81**	−0.80**	−0.69*

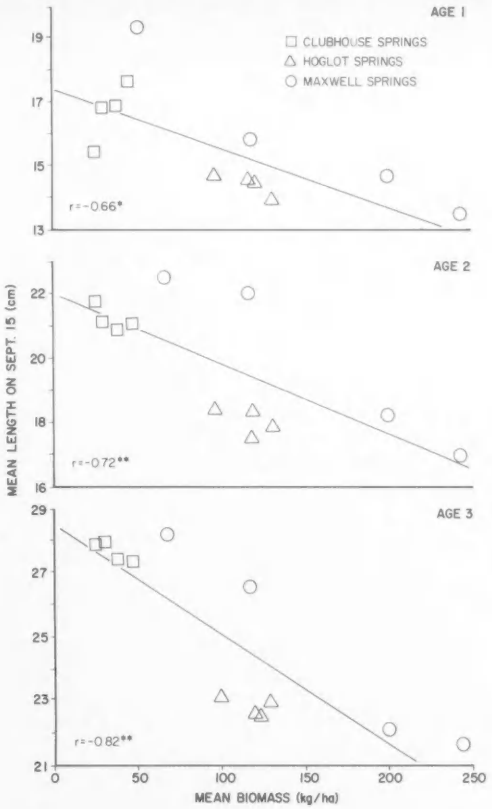

FIGURE 4.—Relationships between mean biomass of all ages of trout and mean lengths of ages 1, 2, and 3 trout on 15 September. (*$P<0.05$; **$P<0.01$.)

TABLE 9.—Annual fishery statistics for brook trout populations in study ponds.

Pond and year	Fishing pressure (angler h/ha)	Total harvest (no./ha)	Catch rate (no./h)	Mean size (cm)	Yield (kg/ha)
Clubhouse Springs:					
1969	1,069	580	0.55	21.8	68.4
1970	1,405	392	0.28	21.4	37.2
1972	809	298	0.37	20.3	27.4
Hoglot Springs:					
1969	835	926	1.11	18.3	54.6
1970	526	391	0.74	19.3	25.4
1972	401	218	0.54	18.8	13.5
Maxwell Springs:					
1969	189	334	1.77	27.2	71.8
1970	154	320	2.08	23.1	39.7

independent variables of fishing pressure and trout biomass in spring ($r = 0.88$; $P<0.05$). Fishing pressure was lowest at Maxwell Springs because the pond was privately owned and public access was restricted. The largest trout (up to 430 mm) were harvested from Maxwell Springs which supported the greatest number of age 4 and older trout. In spring 1969 there were about 530 age 4 and older trout/ha in Maxwell Springs and only 16/ha and 69/ha in Clubhouse and Hoglot springs, respectively.

Age 2 trout made up the major portion of the harvest in Clubhouse and Hoglot springs (Figure 5). In both populations, proportions of age 2 and older trout in the harvest were higher than their proportions in the spring populations, suggesting some size selection by anglers.

The fishery at Maxwell Springs differed significantly from the public ponds in 1969 when age 5 and older trout dominated the catch (Figure 5). Large numbers of age 5 trout were present in spring 1969 and 58% were harvested that season. The owner of Maxwell Springs reported that harvest and fishing pressure in years prior to the study were well below those of 1969 and 1970;

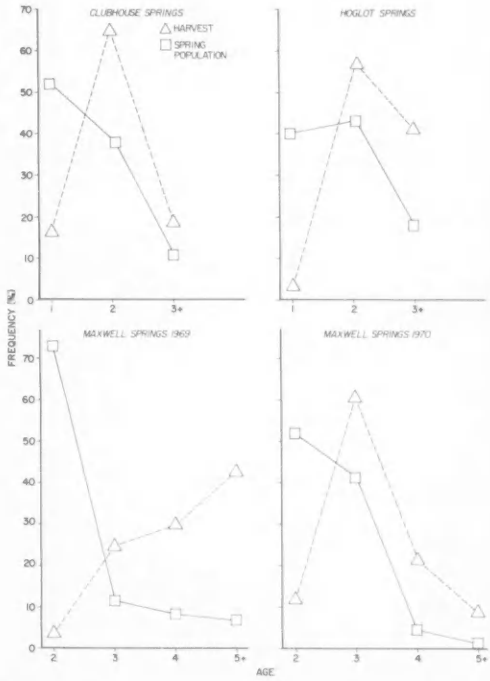

FIGURE 5.—Age-frequency distributions of harvests and populations of legal-sized trout in spring. Data points for Clubhouse and Hoglot springs are means of data from 1968 to 1970, and 1972.

it is likely that the population had been lightly exploited prior to 1969. Results of electrofishing surveys apparently stimulated greater fishing effort. Shape of the 1970 catch-frequency curve resembled those of public ponds, except that substantial numbers of age 4 and older trout were harvested.

Size selection by anglers at Maxwell Springs was reflected in the relative rates of natural and fishing mortality. For ages 2-5 trout, mean total mortality rates from spring to fall increased with age and were paralleled by fishing mortality (Figure 6). Natural mortality changed little with age of fish. Differences between natural and fishing mortality were greatest for age 5 trout and fishing mortality accounted for 69% of their total mortality.

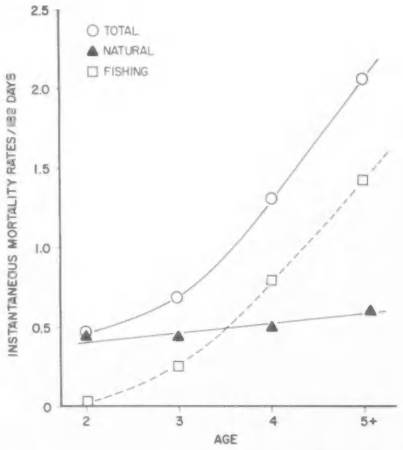

FIGURE 6.—Instantaneous rates of total, fishing, and natural mortality (spring to fall) of ages 2 to 5 trout at Maxwell Springs. Data points are 2-yr means, 1969-70.

Production

Production was most influenced by numbers of fingerlings hatched in ponds and numbers of immigrants. Growth rates varied little among populations, hence year class biomass had the most effect on production. Among populations annual production ranged from 26 kg/ha at Clubhouse Springs to 331 kg/ha at Maxwell Springs (Table 10).

Annual production in Clubhouse Springs was dependent upon biomass of ages 1 and 2 trout. Few fingerlings immigrated into the pond and they contributed only 10% of total annual production. Highest annual production occurred in 1970 when the population was bolstered by high levels of immigration during winter 1969-70 and in summer 1970. Low biomass in spring and below average rates of immigration in 1969 and 1971 resulted in low annual production.

TABLE 10.—Production (kilograms per hectare) by age-group of brook trout in study ponds. Production by age 0 trout during fall to spring intervals covers the period from 1 March to end of interval. Production by age 4 trout includes all older age-groups. Total annual production was expressed in terms of 365 days.

Site and interval	[1]0	1	2	3	4	Total	Annual total
Clubhouse Springs:							
27 Mar. 1968		20.8	11.4	3.9	0.5	36.6	
28 Aug. 1968		1.5	4.4	4.0	—	9.9	45.3
8 Apr. 1969	0.9	5.1	10.8	5.6	1.0	23.4	
8 Sept. 1969		1.8	2.0	1.5	0.6	1.9	25.8
1 Apr. 1970	2.7	17.8	9.4	5.5	1.4	36.8	
8 Sept. 1970		5.7	8.7	6.1	0.8	21.3	54.1
29 Apr. 1971	1.0	5.6	5.2	1.8		13.6	
8 Sept. 1971		1.8	7.2	2.7		11.7	25.9
21 Apr. 1972							
Hoglot Springs:							
2 Apr. 1968	40.1	20.9	32.2	10.6	7.9	111.8	
21 Aug. 1968	9.5	2.9	5.6	13.4	0.3	31.1	141.4
8 Apr. 1969	51.1	21.2	22.7	18.5	4.6	118.1	
8 Sept. 1969	11.3	7.2	3.8	15.5	2.7	40.5	156.4
13 Apr. 1970	56.2	52.9	23.3	11.5	3.0	146.9	
8 Oct. 1970	18.5	6.4	14.7	7.7	1.4	48.7	187.9
28 Apr. 1971	34.8	15.9	35.7	5.9	0.6	92.9	
21 Sept. 1971	14.1	5.1	3.1	10.2	1.3	33.9	125.4
2 May 1972							
Maxwell Springs:							
6 Apr. 1969	97.0	56.8	80.0	17.5	37.0	288.3	
13 Oct. 1969	11.6	10.9	4.9	2.4	1.7	30.2	331.2
26 Mar. 1970	97.5	52.5	38.6	38.7	12.2	239.5	
6 Oct. 1970	34.0	2.8	17.2	20.4	8.6	83.0	297.2
26 Apr. 1971	90.6	17.4	35.3	22.9	6.1	172.3	
20 Sept. 1971	10.6	23.0	1.8	3.1	1.2	39.7	211.4
26 Apr. 1972							

[1]Age at end of interval.

At Hoglot Springs, annual production was most affected by numbers of fingerlings hatched in the pond and numbers of immigrants. Age 0 trout accounted for nearly 32% of average annual production. Annual production peaked in 1970 (Table 10) when large numbers of age 1 trout immigrated oversummer and cohort biomass increased from 13 kg/ha in spring to 91 kg/ha in fall.

Annual production in Maxwell Springs was related to the number of strong year classes present and their subsequent biomasses. The highest annual production was in 1969 when two large age-groups were present (1968 and 1969 year classes), and there was a high biomass of age 2 and older trout (Table 10). In 1971, the year of lowest production, the only large age-group was the fingerlings. In all years, production

of age 0 trout was important; they averaged 44% of the total.

Among populations the influence of age 0 trout on total production was evident when production by individual age-groups was considered in relation to their biomass (Figure 7). Age 0 trout had a marked effect on the slope of the relationship between $\bar{B}$ and P when all age-groups were combined. The linearity of these relationships was due to similarity in growth rates within and among populations. If growth rates had declined with increasing biomass, the relationship between $\bar{B}$ and P would have been curvilinear.

There was no single parameter that could adequately describe levels of recruitment because numbers of trout hatched within ponds and numbers of immigrants were different in each population. If densities of fall fingerlings or spring yearlings were used as indexes of recruitment, mean annual production among populations and recruitment were directly related (Figure 8). Although age 0 trout made up a substantial portion of total production in Hoglot and Maxwell springs, production of just age 1 and older trout was also related to recruitment.

The ratio of annual production to mean annual biomass ($P/\bar{B}$) has been called "turnover rate" and "efficiency of production." The $P/\bar{B}$ ratio is, in fact, the weighted mean growth rate of the population. Population production is the sum of $G \times \bar{B}$ for each year class, hence, dividing total production by the sum of year class biomasses yields population growth rate, weighted according to the biomass of each age-group.

Among populations annual $P/\bar{B}$ ratios for age 1 and older trout varied by more than 100% (Table 11). The $P/\bar{B}$ ratio in 1969 at Clubhouse Springs (0.63) was probably underestimated. Growth rates

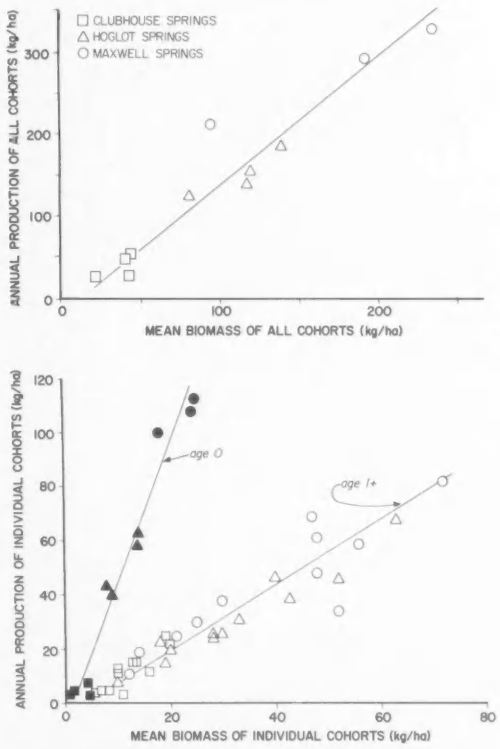

FIGURE 7.—Relationships between mean annual biomass and annual production. Production and biomass of all cohorts are combined in upper panel. In lower panel each point represents a single cohort. Lines fitted by inspection.

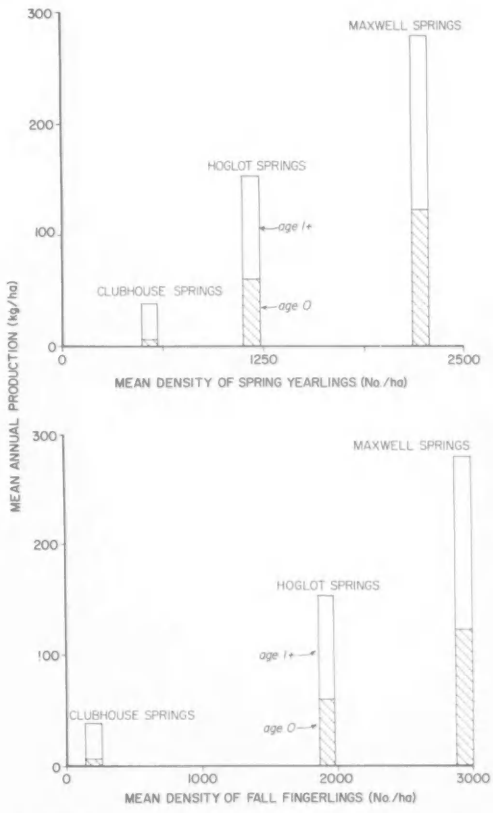

FIGURE 8.—Mean annual densities of spring yearlings and fall fingerlings in relation to mean annual production of age 0 and age 1 and older trout.

TABLE 11.—Total annual production (P), mean biomass ($\bar{B}$), and $P/\bar{B}$ ratios for all age 1 and older brook trout.

Pond and year	P (kg/ha)	$\bar{B}$ (kg/ha)	$P/\bar{B}$
Clubhouse Springs:			
1968	43.4	39.0	1.11
1969	23.0	36.5	0.63
1970	45.7	36.3	1.26
1971	23.0	20.1	1.14
Hoglot Springs:			
1968	89.3	103.1	0.87
1969	95.2	100.0	0.95
1970	110.0	118.2	0.93
1971	71.9	65.9	1.09
Maxwell Springs:			
1969	206.9	199.8	1.04
1970	173.6	162.2	1.07
1971	87.7	64.2	1.37

of individual age-groups during winter 1969-70 were well below average and age 1 trout lost weight. This was the only period in which an age-group in Clubhouse Springs had a negative growth rate, and it was probably due to immigration of yearling trout smaller than pond residents. Overwinter production in 1969-70 was 2 kg/ha; production during other winter periods ranged from 10 to 21 kg/ha.

$P/\bar{B}$ ratios for age 1 and older trout in Hoglot and Maxwell springs tended to decline with increasing biomass (Table 11), i.e., mean weighted growth rates were inversely related to density. As I have noted, age-specific, instantaneous growth rates (G) were the only growth parameters poorly correlated with density. Biased estimates of G for individual year classes could have obscured relationships with population density, but did not markedly affect mean weighted growth rates when all adult trout were combined.

DISCUSSION

Estimation of trout production in this study required several assumptions and the data should be interpreted accordingly. Major assumptions were: 1) numbers of emergent fry were 80% of total egg production, 2) growth and mortality rates of age 0 trout were constant from emergence to fall, and 3) production could be estimated from the product of G and $\bar{B}$ when immigration occurred.

Chapman (1967) suggested that production of brown trout fry in Horokiwi Stream (Allen 1951) could have been overestimated by fourfold due to errors in estimating egg deposition and emergence. I used fecundity data from two populations of wild brook trout that were collected from ponds in the same watershed as the study ponds. Fecundity differences among populations were probably not large since growth rates of the trout were similar. I assumed that all eggs were spawned because egg retention was insignificant in other stream populations of wild brook trout (Wydoski and Cooper 1966). In addition, I assumed emergent fry represented 80% of total egg production. Percentage of live embryos in individual redds exceeded 80% in my study. Brasch (1949) studied brook trout reproduction in several ponds; he found survival from egg to emergence was 79%. In laboratory experiments, emergence of brook trout fry exceeded 80% when the substrate was composed of 5% or less sand and concentrations of dissolved oxygen exceeded 7 ppm (Hausle 1973). Therefore, I do not believe estimates of egg production or emergent fry seriously biased production estimates.

The assumption of constant mortality rates from emergence to fall represents potentially large errors in production estimates for age 0 trout. Hunt (1966) found that instantaneous mortality rates from emergence in February to June were about 10 times greater than mortality from June to September; he based mortality rates on 90% emergence of fry. To assess the influence of variable mortality rates, I calculated production for the 1970 year class at Maxwell Springs from emergence to October with different mortality schedules. If mortality were five times greater during the first half of the interval than during the second, production would have been 63 kg/ha, and if mortality rates varied by tenfold, production would have been 60 kg/ha. With a constant mortality rate from emergence to October, estimated production was 109 kg/ha. Thus, if there was an initial high mortality of fry, production of age 0 trout could have been overestimated by 50 to 60%, and annual production by all age-groups would have been overestimated by 19%.

Assumptions that instantaneous growth rates were constant from emergence to fall certainly oversimplify growth history of fingerlings, but overall effects of this assumption on production estimates did not appear significant. Hunt (1966) found large variations in monthly growth rates of brook trout from emergence to October; growth rates increased to a maximum in May and then declined the rest of the year. Average monthly growth rates from February through April were not different than those from May to October (t-test $P>0.05$). These periods correspond to periods for which I calculated production by age 0

trout. If changes in growth rates of trout fry in my study were similar to those in Lawrence Creek, then assumptions of constant growth rates are much less serious than those regarding mortality rates.

To estimate production with the Ricker formula ($G \times \bar{B}$) one assumes that no emigration or immigration occurred (Chapman 1967). Effects of emigration on production are similar to those of mortality. Recognition of emigration allows one to demonstrate the fate of production, but does not directly affect calculated values. Immigration, however, can have serious effects upon production estimates. The Ricker formula integrates two simultaneous processes, growth and mortality. Numbers of fish are assumed to decrease exponentially and their mean weights are assumed to change in a similar fashion. When immigration occurs and an age-group increases in number, the Ricker formula treats this increase as an exponential one.

To assess the influence of immigration on production, I simulated three different immigration patterns in which year class density increased from 1,400 trout/ha in April to 3,600/ha in October (Figure 9). Curve B represents an exponential increase in density, i.e., that assumed in the Ricker formula. Production was calculated at monthly intervals and the same growth rate was used for each simulation. If all immigration had occurred in the first half of the interval (A), estimation by the Ricker formula would have underestimated production by 30%, and if trout had immigrated in the latter half of the interval (C), production would have been overestimated by 54%. This increase in cohort size was similar to that of age 1 trout in Hoglot Springs in 1970, the largest increase that occurred in either Hoglot or Clubhouse springs. Therefore, potential errors in production estimates for other intervals would have been less serious.

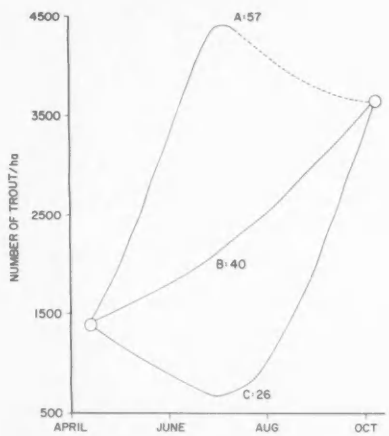

FIGURE 9.—Three hypothetical immigration patterns for a single age-group. Production for each curve was calculated monthly using the same instantaneous growth rate ($G = 0.99$, $t = 0.5$ yr). Total production for each curve is given next to letter designation.

Recruitment, via immigration and spawning within ponds, appeared to be the most important factor influencing production. Even though production by age 0 trout could have been overestimated, production by age 1 and older trout was closely tied to recruitment rates. In other studies, only a few attempts have been made to link production to recruitment. Backiel and Le Cren (1967) analyzed data from Lawrence Creek (Hunt 1966) and Cultus Lake (Ricker and Foerster 1948) and showed that production was directly related to numbers of emerging fry. Highest annual production of sockeye salmon, *Oncorhynchus nerka*, in Lake Dal'neye occurred in years of highest egg deposition (Krogius 1969).

In this study population biomass was determined by annual recruitment. Among populations, production was most influenced by trout biomass because age-specific growth rates were not significantly different. As a result, production increased linearly with biomass. Hunt (1974) found similar linear relationships for brook trout in Lawrence Creek. Backiel and Le Cren (1967) reviewed density effects on production and illustrated both linear and curvilinear associations between production and biomass. Curvilinear relationships resulted when growth rates were severely depressed at high fish densities and in all of these studies fish were stocked and movement was restricted. I am not aware of any study of wild fish populations in which inverse density-dependent growth caused curvilinear relationships between production and biomass. Rather, in wild populations of salmonids, fish densities appear to be maintained at levels that do not result in seriously depressed growth rates and production increases directly with biomass.

Standing crops of harvestable trout (age 1 and older) in the three populations declined over a year's time because total mortality exceeded growth rates, even though immigration bolstered density of some age-groups (Table 12). The actual

TABLE 12.—Comparison of annual yield of brook trout with potential yield and biomass loss to natural mortality. Data are for trout age 1 and older. All values are in kilograms per hectare.

Pond and interval	(1) Annual biomass loss	(2) Annual production	(1 + 2) Potential yield	(3) Actual yield	|(1 + 2) − 3| Biomass loss to natural mortality	Actual/ potential yield (%)
Clubhouse Springs:						
1970-71	31.0	49.7	80.7	68.4	12.3	85
Hoglot Springs:						
1969-70	27.0	89.0	116.0	54.6	61.4	47
1970-71	8.8	114.5	123.3	25.4	97.9	21
Maxwell Springs:						
1969-70	87.9	200.3	288.2	71.8	216.4	25
1970-71	57.8	188.2	246.0	39.7	206.3	16

biomass loss includes both the change in standing crops from one year to the next and the production during that interval. In all three populations, the actual annual loss in biomass exceeded average standing crops. This loss in biomass may be viewed as the potential yield (Table 12). Biomass lost to natural mortality was calculated as the difference between potential and actual yields. Fate of potential yields appeared dependent upon fishing pressure. In Clubhouse Springs fishing pressure was highest (Table 9), and yield in 1970 was 85% of the potential. Only 16 and 25% of potential yields were taken in Maxwell Springs, where fishing pressure was lowest. The relatively low level of exploitation in Maxwell Springs resulted in substantial biomass losses to natural mortality.

Estimates of fish production in lentic waters have varied from less than 1 g/m² to 64 g/m², but in most studies they were <20 g/m² (Le Cren 1972). Highest reported values were for juvenile sockeye salmon in Lake Dal'neye (Krogius 1969). Production estimates for Maxwell Springs (21-33 g/m²) are among the highest values currently available. Even if contributions of age 0 trout in Maxwell Springs are ignored, production estimates still rank high (11-22 g/m²). Carline and Brynildson (1977) suggested that high levels of trout production in ponds similar to Maxwell Springs were due to extensive littoral areas and high standing crops of benthic organisms. While prevailing food densities determine the level of potential fish production, attainment of this potential level is dependent upon annual recruitment of some minimum number of fish.

In this study differences in spawning areas among ponds were obvious and trout production varied accordingly. In many instances quantity and quality of spawning sites are unknown or cannot be readily determined. Where recruitment is limiting, fish production will be relatively low, regardless of the water's general productivity. If production is to be used as a measure of a system's capacity to support species of interest, recruitment of that species should be at or near maximum levels.

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KOKO HEAD, OAHU, SEA-SURFACE TEMPERATURES AND SALINITIES, 1956–73, AND CHRISTMAS ISLAND SEA-SURFACE TEMPERATURES, 1954–73

GUNTER R. SECKEL[1] AND MARIAN Y. Y. YONG[2]

ABSTRACT

Sea-surface temperatures and salinities have been collected twice weekly at Koko Head, Oahu, Hawaii, since 1956; and at Christmas Island in the central equatorial Pacific, sea-surface temperatures have been collected daily since 1954. In 1971, Seckel and Yong used harmonic analysis as a curve-fitting method to bring these observations, 1 yr at a time, through 1969, into a form useful for descriptive and numerical applications. In this paper the analyses are updated through 1973 and the method is used to describe the entire data series.

The data series have been separated into several scales of variability: long-term variability (periodicities larger than 1 yr), short-term variability (12-mo and shorter periodicities), average annual cycle (the 12-, 6-, 4-, and 3-mo periods), and the residual variability that characterizes individual years (the short-term variability with the annual cycle removed). In contrast to the Koko Head temperature where the annual cycle predominates, the interannual variability predominates, at times obscuring the annual cycle, in the Koko Head salinity and Christmas Island temperature. The interannual change of the Koko Head salinity can be about three times, and that of the Christmas Island temperature can be about four times the average annual variability. In the average annual temperature and salinity cycles at Koko Head the amplitudes of the 6-, 4-, and 3-mo periods are small in relation to the 12-mo period. In the average annual temperature cycle at Christmas Island, however, the amplitude of the 6-mo period is almost one-half that of the 12-mo period. The residual variations exhibit changing amplitudes and periodicities at intervals of more than 1 yr that resemble amplitude and frequency modulations.

Speculations are made about processes that contribute to the temperature and salinity variations. It appears that in addition to the heat exchange across the sea surface, advection contributes materially to the observed changes at Koko Head and Christmas Island.

Harmonic coefficients resulting from the analyses are listed in the appendices to facilitate reproduction of the data presented.

In an earlier paper, Seckel and Yong (1971) used harmonic analysis as a curve-fitting method, bringing rapidly into usable form regularly sampled sea-surface temperatures and salinities. Analyses were made of sea-surface temperature and salinity obtained once or twice weekly from 1956 to 1969 at Koko Head, Oahu (lat. 21°16′N, long. 157°41′W,), and of sea-surface temperature obtained daily from 1954 to 1969 at Christmas Island (lat. 1°51′N, long. 157°23′W). The temperature and salinity variations for each year were then specified by sets of harmonic coefficients and phase angles. Values calculated at 15-day intervals from the resulting annual functions were used in long-term analyses of the entire data records. These analyses showed that interyear differences in the Koko Head salinity and Christmas Island temperature were larger than seasonal changes.

The long-term changes in surface properties reflect climatic scale ocean-atmosphere processes and, in turn, affect these processes. The changes in properties and processes affect life in the sea. For example, the Koko Head salinity changes indicate primarily changes in the advection produced by variations in ocean circulation (Seckel 1962). It was postulated that changes in circulation also affect the concentration and, therefore, the availability of skipjack tuna caught in Hawaii (Seckel 1972).

The long-term changes in the Christmas Island temperatures are linked with large-scale (at least ocean-wide) ocean-atmosphere processes. Bjerknes (1969) related anomalously high tem-

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peratures and high precipitation at Canton Island in the central equatorial Pacific with intensification of the Hadley circulation and changes in the "southern oscillation." Quinn (1974) related an index of the southern oscillation (the difference of atmospheric pressure between Easter Island and Darwin, Australia) with El Niño phenomena and abnormally high rainfall in the equatorial Pacific. One of the latter is the failure of the Peruvian anchovy fishery. The large interyear differences of equatorial sea-surface temperatures undoubtedly affect the biota in as yet undescribed ways.

It is of value, therefore, to bring the results of monitoring into a form that is useful for fishery applications. Toward this objective we have 1) updated our previous Koko Head and Christmas Island analyses through 1973; 2) analyzed the long series (18 yr for Koko Head, 20 yr for Christmas Island) and separated changes into long-term variability, the annual cycle, and the short-term variability that characterizes individual years; and 3) speculated about the processes that affect the changes evident in the data records.

THE 1970-73 UPDATE

Sampling and Processing

Koko Head, where bucket samples for temperature and salinity determinations were taken twice weekly, is located at the exposed, eastern shore of Oahu. At this location, cliffs extend into the water, and temperature and salinity samples have been found to be representative of offshore conditions. At Christmas Island, bucket temperatures were obtained daily near the plantation village on the ocean side of the lagoon entrance. Measurements were made during the morning at each location.

The procedures used to derive the harmonic coefficients for the 1970-73 observations were the same as those described by Seckel and Yong (1971). Fourier analysis was performed on the residuals from a linear fit so that the temperatures and salinities are expressed as a function of time, t, by

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n) \ldots \quad (1)$$

where $K = F(t_0) + \frac{A_0}{2}$, $\omega = \frac{2\pi}{T}$, and k is the highest harmonic in the series. $F(t_0)$ is the first observed value, A_0 is the Fourier coefficient for $n = 0$, C_n are the coefficients for $n \neq 0$, and α_n are the phase angles. b is the slope of the straight line joining the first and last observations of the fundamental period, T.

The fundamental period for the Koko Head analyses was 365 days. For the Christmas Island analyses the fundamental periods were 120 which for a full year followed in sequence with a 30-day overlap from Julian day 1 to 20, 91 to 210, 181 to 300, and 271 to 390 extending 25 days into the following year.

Results

Results of the analyses for the update years are presented in the appendices. Coefficients and phase angles for the Koko Head temperatures and salinities are found in Appendix A, Tables 1 and 2. Figures of the expected values computed from the harmonic functions together with the observed values for the Koko Head temperatures and salinities are found in Appendix B, Figures 1 and 2. The coefficients and phase angles for the Christmas Island temperatures are found in Appendix C, and the plotted functions together with the observed values are found in Appendix D.

Standard errors of estimate for the fitted Koko Head temperatures and salinities and Christmas Island temperatures are listed in Appendix E, Tables 1, 2, and 3, respectively.

Christmas Island Data Problems

Observer problems at Christmas Island caused the sea temperature sampling to be interrupted from May 1972 to April 1973. The data gap was reduced by Hawaii Institute of Geophysics (HIG) bucket temperatures obtained daily since November 1972 near the airport on the northeast shore of the island. Although NMFS (National Marine Fisheries Service) sampling resumed in April 1973, HIG data were used in our analysis for the entire year. In our long-term analysis the remaining data gap between May and November 1972 was closed by linear interpolation. Mean monthly temperatures obtained from the two sampling sites indicate that NMFS temperatures are on average about 0.5°C lower than the HIG values (Table 1). The HIG data have not been adjusted to reflect this temperature difference.

The large scatter of data at Christmas Island

TABLE 1.—Mean monthly sea-surface temperature (°C), Christmas Island: National Marine Fisheries Service station (NMFS) and Hawaii Institute of Geophysics station (HIG).

	Date	NMFS	HIG
1973	May	26.6	26.2
	June	24.7	25.6
	July	23.6	25.2
	August	23.9	24.5
	September	23.8	24.1
	October	23.4	23.8
	November	23.0	23.3
	December	23.4	23.5
1974	January	23.9	24.0
	February	24.1	24.3
	March	24.6	24.7
	April	24.7	25.2
	May	23.9	24.9
	June	23.6	25.0
	Average	24.1	24.6

in comparison with that at Koko Head indicates another data problem. The scatter probably is caused by sampling of water in the shallow beach area that is more sensitive to changes in the local heating-cooling processes than the deep water of an offshore site.

Finally, there are no systematically observed sea-surface temperatures near Christmas Island against which the shore measurements can be calibrated. However, the monthly pamphlet *Fishing Information*[3] contains a temperature chart for the equatorial Pacific. Contours near Christmas Island are based on insufficient observations to reproduce the temperature distribution reliably. Therefore, the values from these charts, plotted on the annual graphs of Appendix D, show large variations in the difference between the *Fishing Information* temperatures and Christmas Island observations. On average the *Fishing Information* values are 1.3°C higher than the midmonth expected values with differences ranging from −1.2° to 4.1°C.

The discrepancy between the temperature sets, in part, may be due to a tendency toward a warm bias of merchant vessel temperature reports. More probable, however, Christmas Island temperatures, being measured in the morning, reflect the effect of night cooling in shallow water that would be in excess of the temperature decline taking place in deeper, offshore water.

Despite the apparent discrepancies between the beach and offshore temperatures, the data from the shore sampling sites reflect climatic scale anomalies. For example, both the Christmas Island record (Seckel and Yong 1971) and the Canton Island record (Bjerknes 1969) show the equatorial cold anomaly of 1955-56, the warm anomaly of 1957-58, and the anomalous biannual temperature variations of 1963-67.

ANALYSES OF LONG-TERM DATA RECORDS

In this section we present harmonic analysis results of the entire data series and separately display the long-term variability, the short-term variability, the average annual cycle, and the variability that characterizes individual years.

The entire data series is expressed by the function

$$S_L = A + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n) \ldots \quad (2)$$

where A gives the average value of the series, k is the highest harmonic of the analysis, and other symbols have the same meaning as given for Equation (1).

Input values for these analyses were calculated at 15-day intervals from the annual analyses presented in this and our previous paper (Seckel and Yong 1971). Analysis of the 1956-73 Koko Head data was carried to the 72d harmonic and of the 1954-73 Christmas Island data to the 80th harmonic so that the shortest period resolved in each series is 3 mo. Analyses were carried out on the residuals from a linear fit as in the analyses of the annual data sets. The harmonic and linear coefficients for the long-term series are listed in Tables 1, 2, and 3 of Appendix F.

The fitted curves resulting from these analyses together with the input values are shown in panels A of Figures 1, 2, and 3. Dominant in the Koko Head temperature is the annual variation without pronounced longer term trends other than the rise of maximum and minimum temperatures from 1966 to 1968. In contrast to the Koko Head temperature curve, the salinity curve shows longer term variations that are larger than the seasonal variations. Also, during some years such as in 1957, annual variation is not apparent. The Christmas Island temperatures convey a similar picture; interannual changes are larger than the annual changes. Again, the latter may be obscured or absent as during the years 1963-66 and in 1973 when biannual changes dominated.

[3] *Fishing Information*. March 1970 through December 1973. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., La Jolla, Calif.

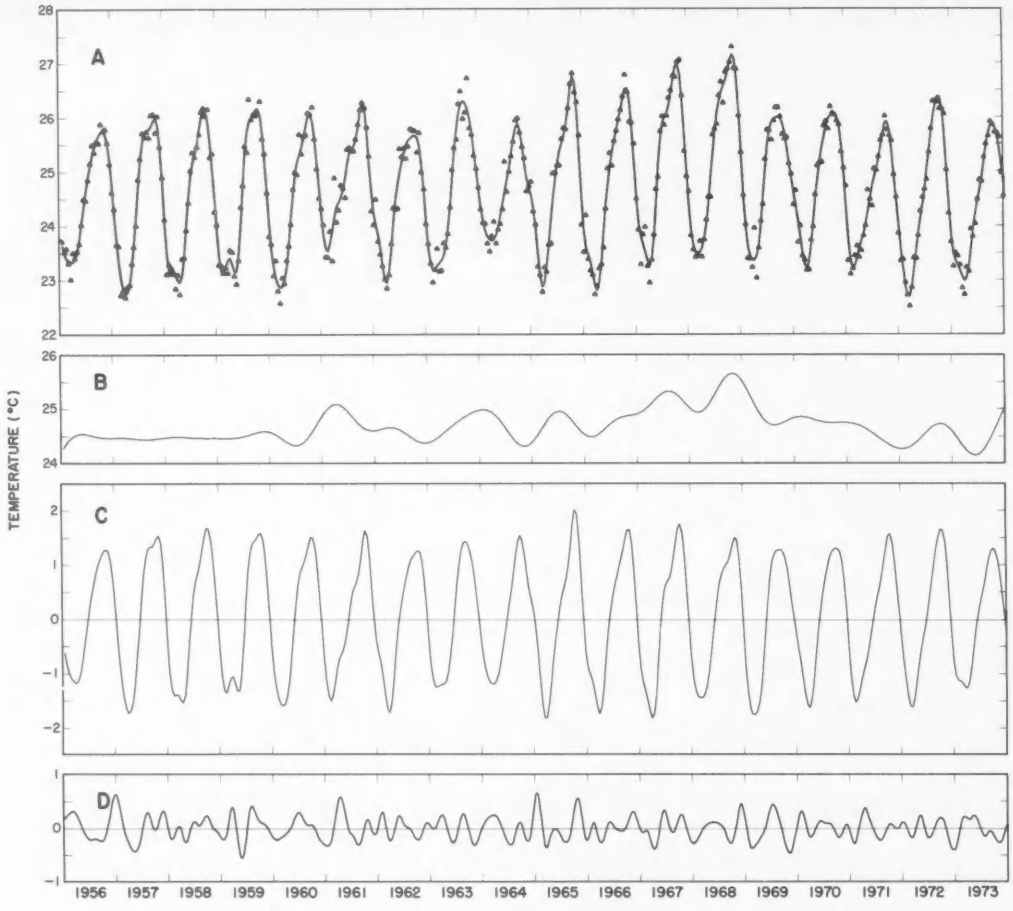

FIGURE 1.—Koko Head temperature, 1956-73: A. Fitted curve with a 3-mo resolution (n = 1-72). B. Long-term variation (n = 1-17). C. Short-term variation (n = 18-72). D. Residual variation (n = 19-35, 37-53, 55-71).

The amplitudes (C_n) of the long-term analyses (Figure 4) confirm these qualitative impressions. In the Koko Head temperature, the amplitude of the annual sinusoid (18th harmonic) is dominant and almost six times as large as the largest amplitude of the long periods. In the Koko Head salinity and Christmas Island temperature, on the other hand, long periods have the largest amplitudes. For the Koko Head salinity the amplitude of the fourth harmonic is larger than that of the annual sinusoid and for the Christmas Island temperature the amplitude of the first harmonic is almost twice that of the annual sinusoid.

Long-Term Changes

When long-term changes are of interest, the annual and shorter term variability can be filtered by a variety of methods including the commonly used 12-mo moving average method. After harmonic analysis has been used as a curve-fitting technique, however, it is simple to evaluate only the terms in the harmonic function up to but not including the annual sinusoid in order to display long-term changes. Thus, in Equation (2), the Koko Head temperatures and salinities were evaluated for n = 1 to 17 and the Christmas Island temperatures for n = 1 to 19. The resulting

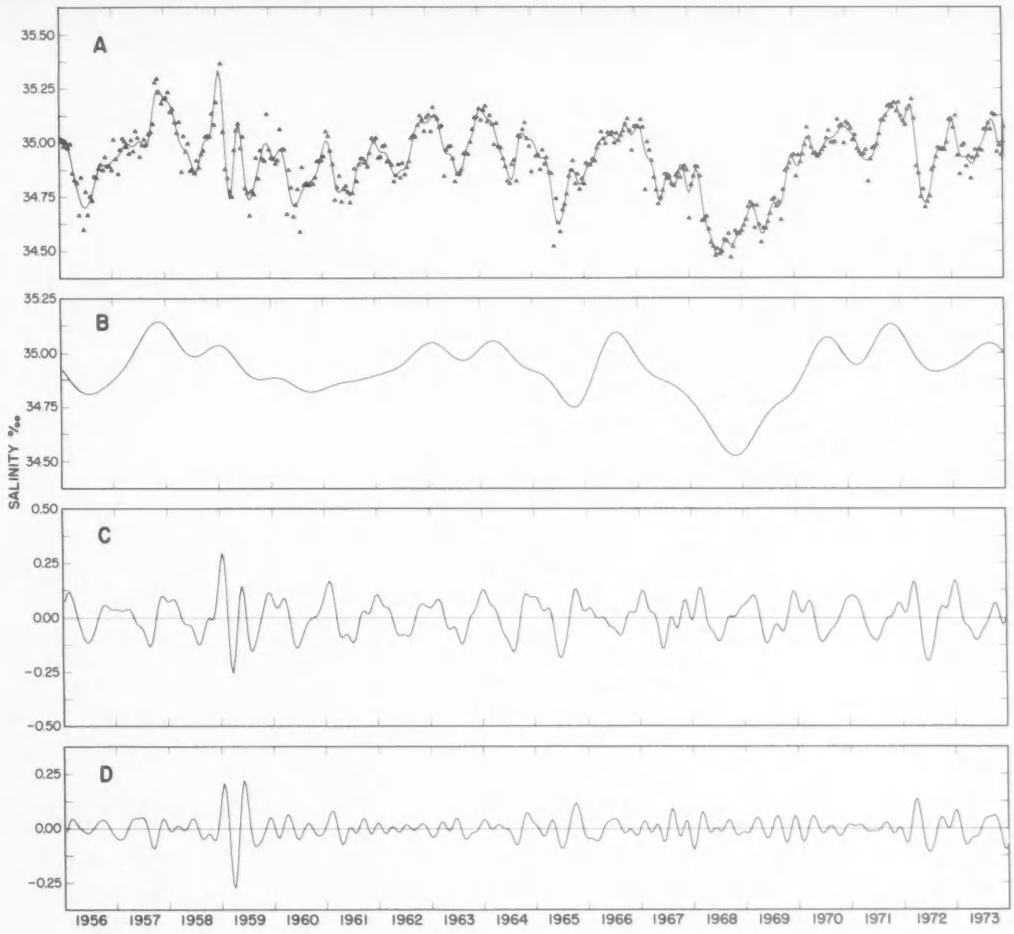

FIGURE 2.—Koko Head salinity, 1956-73: A. Fitted curve with a 3-mo resolution (n = 1-72). B. Long-term variation (n = 1-17). C. Short-term variation (n = 18-72). D. Residual variation (n = 19-35, 37-53, 55-71).

curves are shown in panels B of Figures 1, 2, and 3.

In the Koko Head temperature little variation due to the longer period harmonics is apparent until 1960 when perturbations of 0.5° to 1°C began. A rising temperature trend between 1966 and 1968 was followed by a decline to a pre-1960 temperature level. Both the Koko Head salinity and Christmas Island temperatures show the large perturbations previously noted. At Koko Head a pronounced salinity decline began in 1966, reaching almost 34.5‰ in 1968 before rising again to a range near 35‰. Times of high Christmas Island temperatures stand out. A prominent feature is the pronounced temperature decline during 1973 from one of the highest values to the coldest temperatures observed during the 20 yr of our record.

Short-Term Changes

The short-term changes relative to the long-term trends are another scale of interest that can be obtained by subtracting the moving average or the long-term values of the previous section from the monthly observations. In our case, and

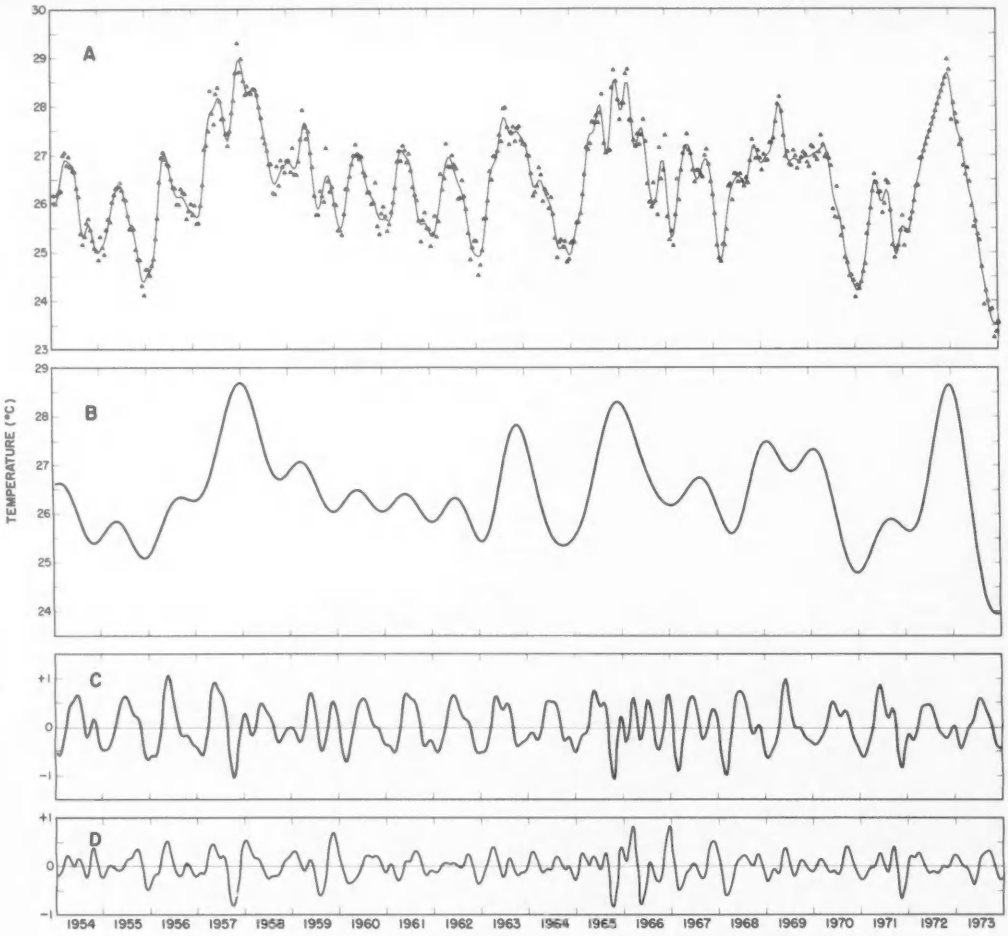

FIGURE 3.—Christmas Island temperature, 1954-73: A. Fitted curve with a 3-mo resolution (n = 1-80). B. Long-term variation (n = 1-19). C. Short-term variation (n = 20-80). D. Residual variation (n = 21-39, 41-59, 61-79).

when variations of <3 mo need not be resolved, it is simple to display short-term changes by evaluating the higher harmonics in Equation (2) beginning with the annual sinusoid (n = 18-72 for Koko Head, n = 20-80 for Christmas Island). The resulting curves are shown in panels C of Figures 1, 2, and 3.

The Koko Head temperature curve looks similar to the initial harmonic fit (Figure 1A) because the long-term changes are small in comparison to the annual variations. In the case of the Koko Head salinity and the Christmas Island temperature, the annual variations that during some years were obscured by the long-term trends are clearly apparent. At Koko Head low salinities occur during spring and summer and high salinities during fall and winter. At Christmas Island high temperatures occur in late spring and low temperatures in fall or winter.

Annual Sinusoid and Its Harmonics

Evaluation of the annual sinusoid and its harmonics yields the mean annual variation. For annual analyses the harmonics n = 1, 2, 3, and 4 have periods of 12, 6, 4, and 3 mo. For the 18-yr

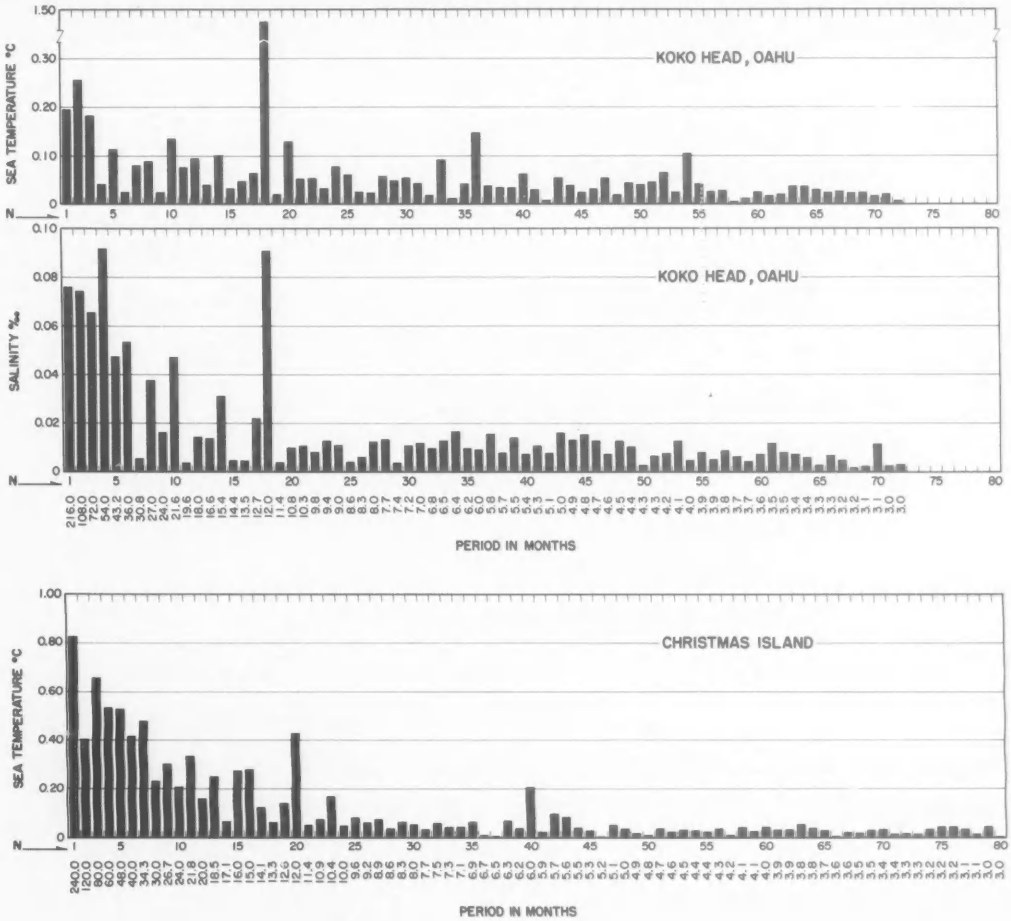

FIGURE 4.—Absolute magnitude of amplitudes of the long-term harmonic functions for Koko Head temperatures, 1956-73; Koko Head salinities, 1956-73; and Christmas Island temperatures, 1954-73.

Koko Head series, these periods are given by $n = 18, 36, 54$, and 72; and for the 20-yr Christmas Island series, they are given by $n = 20, 40, 60$, and 80. The mean annual variations evaluated from Equation (2) are shown in Figure 5 panels A, B, and C.

The mean annual temperature range of 3°C at Koko Head is about twice the long-term range. In contrast, the mean annual salinity range is 0.2‰ and only about 30% of the long-term range. At Christmas Island the mean annual temperature range is 1°C and only one-quarter of the long-term range.

At Koko Head the annual sinusoid, although visibly modified, dominates the mean annual changes. In both the temperature and the salinity, the amplitude of the annual sinusoid is an order of magnitude larger than that of the 6-, 4-, and 3-mo sinusoids (Figure 4). In the case of the temperature, the interference pattern of the 6- and 4-mo sinusoids is such that during the first half of the year the annual sinusoid is not visibly affected. Constructive interference by these sinusoids depresses the annual sinusoid by about 0.2°C in August, which causes first an increase by that amount in October and then a decrease by the end

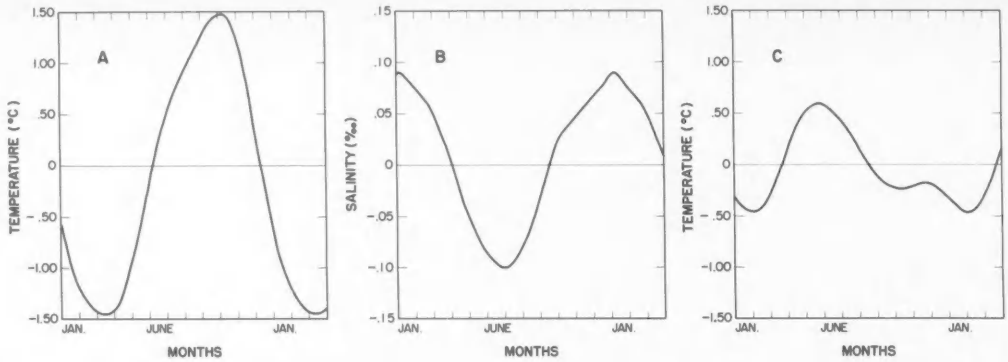

FIGURE 5.—Mean annual variations: A. Koko Head temperatures (n = 18, 36, 54, 72). B. Koko Head salinities (n = 18, 36, 54, 72). C. Christmas Island temperatures (n = 20, 40, 60, 80).

of the year. Consequently, the mean annual curve reflects the temperature trends evident in individual years in that warming lasts between 1 and 2 mo longer than cooling and the cooling rate is higher than the warming rate.

Departures of the mean annual salinity variation from the annual sinusoid, evident in Figure 5B, are not significant.

In contrast to the Koko Head spectra, the amplitude of the 6-mo sinusoid at Christmas Island is large enough to produce a significant modification of the annual sinusoid (Figure 5C). The absolute amplitudes of the 12-, 6-, 4-, and 3-mo sinusoids are 0.43°, 0.21°, 0.04°, and 0.003°C, respectively. Thus, the mean annual temperature variation at Christmas Island has the typical interference pattern produced by a 12- and a 6-mo sinusoid as illustrated in Figure 6. The residual curve, namely the difference between the mean annual curve and the annual sinusoid, is approximately the 6-mo sinusoid.

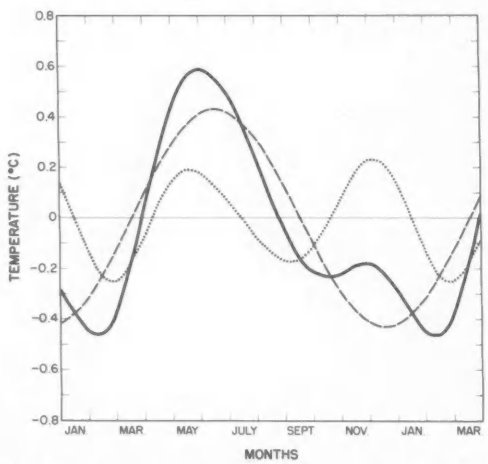

FIGURE 6.—Interference patterns of sinusoids for mean annual variation at Christmas Island. Solid line – n = 20, 40, 60, 80; dashed line – annual sinusoid (n = 20); dotted line – remaining variation (n = 40, 60, 80).

Residual Variations

The dominant feature in the short-term curves (panel C of Figures 1, 2, 3) is the annual variation superimposed upon which is the variability that characterizes each year. This "residual" variability is obtained by evaluating in Equation (2) the short-term variability without the annual sinusoid and its harmonics (n = 19-35, 37-53, and 55-71 for Koko Head, and n = 21-39, 41-59, and 61-79 for Christmas Island). Residual variability is shown in panel D of Figures 1, 2, and 3.

The residual curves are the interference pattern produced by all the sinusoids used in the evaluation. The irregular amplitudes and periodicities occurring at intervals of more than 1 yr give an impression of amplitude and frequency modulations. For example, in the Koko Head salinity curve, relatively large perturbations occur in groups during 1959, 1964-65, 1967-68, 1969-70, and 1972-73. In the Christmas Island residual temperature curve, relatively large perturbations during 1955-60 are followed by smaller perturbations during 1960-65 and by larger perturba-

tions again during 1965-68. These modulations are of a long-term nature but do not appear to be related with the variations shown in panel B of Figures 1, 2, and 3.

On the Separation of Variability Into Various Time Scales

Although there are a number of curve-fitting procedures such as were reviewed by Holloway (1958), we have found Fourier analysis to be a convenient method for the Koko Head and Christmas Island time series. The filtering described above is a byproduct of this method and serves interpretive and descriptive purposes.

Although the moving average method is not recommended for climatological time series,[4] it is commonly used. For this reason, curves obtained by the moving average and the harmonic analysis methods are compared in Figures 7 and 8. The long-term as well as the residual curves of the two procedures are similar though not identical. The amplitudes of the long-term variations are larger in the curves derived by harmonic analysis than in those derived by the moving average method. This difference is to be expected because, in contrast to the harmonic method, input values in the moving average method are weighted equally.

The examples in Figures 7 and 8 were chosen because they illustrate limitations, in terms of physical interpretations, of the filtering techniques. A time series of the sea-surface temperature (salinity) is the signature of processes that govern the observed changes. What information about the governing processes, then, can be inferred from the time series? For example, is the observed change of temperature the result of an anomaly in the local heat exchange across the sea surface and advection produced by the local wind driven current, or is this temperature change a part of a larger scale change with the local processes remaining normal? The examples in panel B of Figures 7 and 8 exhibit variations with an annual periodicity during 1957 in the Koko Head salinity and during 1963, 1964, and 1965 in the Christmas Island temperature although this periodicity is not apparent in panel A of Figures 2 and 3. In these cases were annual variations, such as produced by annually varying processes, present or were they absent?

In the case of the moving average method, 2 yr of data are required to provide the smoothed curve for a single year. At Koko Head the normal mid-year declines in salinity occurred during 1956 and 1958, affecting the shape of the smoothed 1957 curve. Consequently the residual curve showed an annual variation during 1957 (Figure 7B). At Christmas Island (Figure 8B), the residual temperature curve during 1964 also exhibits an annual variation, a maximum in spring and a minimum in fall, although no seasonal trends were indicated during the adjacent years (Figure 3A). In this case, was the normal annual variation in temperature present but obscured by the long-term trend?

In the harmonic analysis procedure the dominant signal in the annual variation is produced by the annual sinusoid. The amplitude of this period is determined by all the data in the series and contributes the same amount to the short-term variations of every year shown in panel C of Figures 1, 2, and 3. For example, a time series could be synthesized by combining a long-term variation with one that has an annual periodicity

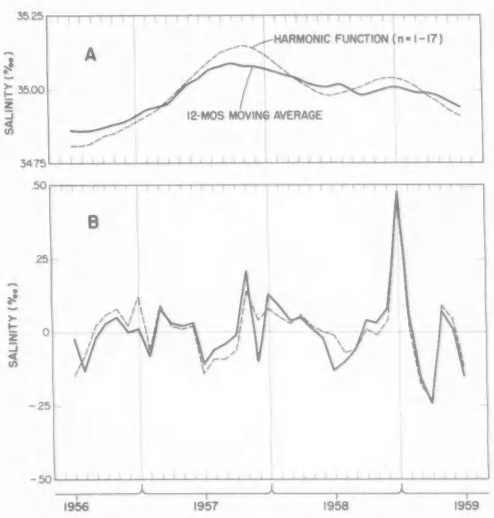

FIGURE 7.—Koko Head salinity, 1956-59: A. Long-term variation produced by 12-mo moving average and by harmonic function (n = 1-17). B. Short-term variation (monthly input values minus long-term values). Solid line — 12-mo moving average; dashed line — harmonic function (n = 1-17).

[4]Climate change. Tech. Note 79, WMO-No. 195, Tp. 100. Secr. World Meteorol. Organ., Geneva, Switz., 1966, 79 p.

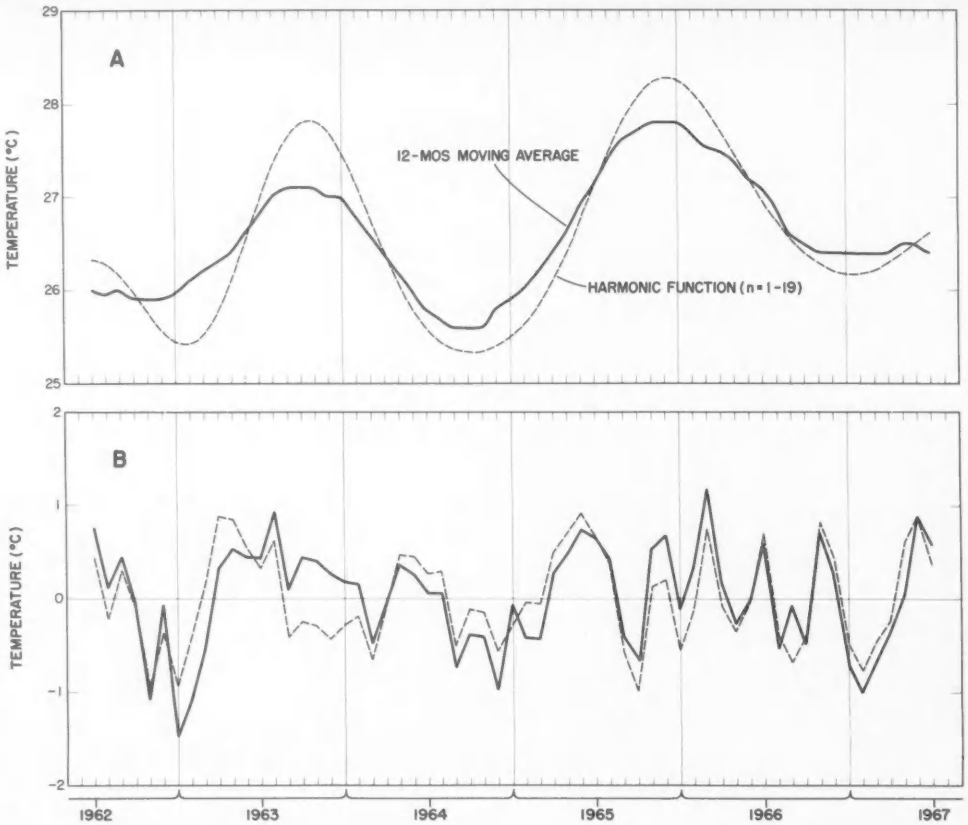

FIGURE 8.—Christmas Island temperature, 1962-67: A. Long-term variation produced by 12-mo moving average and by harmonic function (n = 1-19). B. Short-term variation (monthly input values minus long-term values). Solid line — 12-mo moving average; dashed line — harmonic function (n = 1-19).

every second year. After harmonic analysis and separating the hypothetical curve into a long-term and a short-term variation, the latter would exhibit an annual periodicity during every year.

Thus, the mathematical procedure cannot answer the questions posed above. The procedures illustrated in Figures 7 and 8 as well as other procedures, separate the scales of variability but there is no basis for inferring that the long-term changes are related with, possibly, ocean-wide processes and short-term changes with local processes. Only if the local processes are measured is there a physical basis for the separation into different scales of change.

Speculations About Temperature and Salinity Variations

It is not the purpose of this paper, and the information is not available, to investigate the causes for the temperature and salinity variations that have been described. Nevertheless, such an investigation would further an understanding of the fishery environment as well as the ocean-atmosphere linkages. It is useful, therefore, to speculate about the processes affecting changes in surface properties.

In Hawaiian waters air-sea interaction processes and advection appear to dominate the local

change of temperature and salinity (Murphy et al. 1960; Seckel 1960, 1962). Advection is the product of the surface temperature (salinity) gradient and the component of the current normal to the isotherm or salinity isopleth. Generally near Hawaii the temperature increases and the salinity decreases equatorward. Consequently, with a northward component of flow, advection would increase the temperature and decrease the salinity at Koko Head.

The usual spring salinity decline at Koko Head is best explained by advection. It is estimated that at the latitude of Hawaii there is an excess of evaporation over precipitation with the highest excess occurring during spring and summer (Seckel 1962). Thus, since the salinity is increasing with depth, the only source of lower salinity water lies south of the islands.

On average the orientation of isotherms is northwest-southeast and that of salinity isopleth is zonal. In this case only the meridional component of flow causes salt advection, but both meridional and zonal components of flow cause heat advection. Consequently, meridional components of flow causing salinity variations do not necessarily produce temperature variations. Coincident changes of salinity and temperature that appear to be advection related, tend to occur during late winter and early spring when the North Equatorial Current is weak. For example, between days 60 and 110 of 1973 (Appendix B), decreasing and increasing temperatures corresponded with increasing and decreasing salinities. Pronounced coincident temperature and salinity variations occurred during the first half of 1959 and are most evident in the residual curves, panel D of Figures 1 and 2.

Coincident changes in temperature and salinity during specific seasons are not necessarily associated in the longer term. From 1956 through 1959 when the long-term salinity variations were pronounced, there was no long-term temperature change (panel B of Figures 1, 2). Later, a strong salinity decline lasting from 1966 to 1968 corresponded with a temperature increase. Then, as the salinity returned toward 35‰, the temperature also returned to the pre-1965 values. The first situation may mean that there were climatic shifts in the general northwest-southeast direction, parallel to the isotherms, thus causing a long-term change in the salinity but not in the temperature. In the second situation the climatic shift was first northward and then southward, affecting both temperature and salinity.

White (1975) described secular changes in baroclinic transport and morphology of the North Pacific subtropical gyre and indicated that during the years of low maximum transport the southwest portion of the gyre extended farther south than during the years of large transport. Similarly, it is possible that higher baroclinic flow and tightening of the gyre near Hawaii will result in lower salinity and a relaxation of flow will result in higher salinity. The long-term changes in the Koko Head salinity do not correspond with the changes described by White and are only in partial agreement with the supposition when tested against Wyrtki's (1974) North Equatorial Current index. The supposition, therefore, is in error or, the local wind induced surface flow, superimposed on the baroclinic flow, plays an important part in the long-term salinity changes.

At Christmas Island, in addition to the heat exchange and advection, the effect of wind-induced equatorial divergence is a process affecting the sea-surface temperature. Unfortunately, meteorological observations suitable for the calculation of heat exchange across the sea surface were not made on the island. Estimates made by Wyrtki (1966) and Seckel (1970) indicate the net heat exchange across the sea surface near Christmas Island to lie in the range of about 100 to 300 cal cm^{-2} day^{-1}. Assuming that the heat is distributed through a column of water 50 m deep, this process can produce temperature changes from about 0.6° to 1.8°C/mo. Temperature increases within this range are observed (Figure 3A).

An important term in the net heat exchange is the radiation from sun and sky that is affected in the equatorial region of the central Pacific by large variations in cloudiness (Bjerknes et al. 1969). The effect of such variability is most pronounced in late fall and early winter (Seckel 1970, figure 6). For example, the average net heat exchange near Christmas Island for November 1963 to January 1964 was calculated to be 177 cal cm^{-2} day^{-1}, and for the same months 1 yr later, 274 cal cm^{-2} day^{-1}. The average calculated radiation from sun and sky during the same periods was 372 cal cm^{-2} day^{-1} and 440 cal cm^{-2} day^{-1}, respectively, and accounted for 70% of the interyear difference in the net heat exchange. The Christmas Island water temperature declined in the

first and rose in the second of these years (Figure 3A).

Heat gain across the sea surface cannot produce a temperature decline and, therefore, other processes must affect the temperature. One of these processes is heat advection that, at the Equator, is the product of the zonal current and the zonal temperature gradient. A raft designed for underwater biological observations was set out in February 1964 near the Equator at about long. 150°W and drifted westward 1,084 km (585 n.mi.) in 194 h (Gooding and Magnuson 1967) giving an average speed of 155 cm s^{-1}. A current with the speed of the raft, given a zonal temperature gradient of 0.5°C/10° of longitude, would produce a temperature change of more than 1.8°C/mo. A slower surface current, 30 cm s^{-1}, was observed on the Equator at long. 140°W during April 1958 (Knauss 1960). This current with the same zonal temperature gradient as before would produce a temperature decline of about 0.4°C/mo.

The South Equatorial Current indices presented by Wyrtki (1974) reflect large variability in the zonal current such as cited above. Additionally, monthly charts of sea-surface temperature (Eber et al. 1968) show the zonal gradient at the Equator to range from zero to >1°C/10° of longitude. Advection, therefore, is expected to play a large role in the temperature variations observed at Christmas Island.

Near the Equator the wind field is a key element in the evaporative heat loss, the cloudiness (affecting the radiation flux across the sea surface), upwelling, and in driving the equatorial currents. Quinn's (1974) southern oscillation (SO) index is related to the central South Pacific trade winds. It is not surprising, therefore, to find coherence in the changes of the SO index, Wyrtki's current index, and the Christmas Island temperature. Selecting the pronounced features of Figure 3B, declining SO index values during 1956, 1963, 1965, 1968, and 1971-72 correspond with rising temperatures. Increasing index values during 1964, 1966, and 1970 correspond with declining temperatures. During the first series of years South Equatorial Current speeds are declining and during the second series they are increasing.

SUMMARY

In this paper we have used harmonic analysis to make Koko Head temperature and salinity time series and Christmas Island temperature time series available for descriptive as well as numerical applications.

Time series data can be treated by a number of mathematical procedures in order to elicit important information. Initially, however, the presentation of the data in graphical form is most useful. The graphs in the appendices indicate the nature of the annual variations, and Figures 1, 2, and 3 indicate the nature of the long-term variations.

Although spectral analysis is not the objective of our work, the curve-fitting procedure further serves the descriptive purposes in that it permits separation of the time series into different scales of variability (panels B, C, D of Figures 1, 2, 3). For example, at Christmas Island the interannual temperature variation is as much as four times the average annual variation (Figures 3B, 5C). Equivalent figures of Koko Head salinity show that the interannual change can be about three times as large as the average annual variation.

Results of our analyses are also useful in numerical applications. Coefficients and phase angles (Appendices A, C, F) rather than observed values can be used for further calculations. In this manner the sampling variability apparent in the graphs of Appendices B and D is filtered out and variations of undesired duration can be omitted.

The separation of the time series into different scales of variability is a mathematical procedure and physical inferences must be made with caution. For example, Figures 2C and 3C show an annual cycle during every year although no annual cycle was apparent during 1957 in Figure 2A or during 1963, 1964, and 1965 in Figure 3A. The procedure does not indicate whether during these years the processes producing the annual cycle were absent or whether they were present but obscured by other processes. In another example, a 12-mo and a 6-mo sinusoid combine to reproduce the mean annual temperature cycle at Christmas Island. Again, the procedure does not indicate whether there exists a process affecting the temperature with a 6-mo periodicity.

Available information indicates that advection is an important process affecting the observed temperature and salinity variations. At Christmas Island large changes in the zonal component of the South Equatorial Current appear to cause large variations in advection. At Koko Head changes in the North Equatorial Current (Wyrtki

1974) do not correlate with the salinity changes, and variations in the meridional component of flow appear to cause the seasonal and long-term salinity changes.

On the basis of the long-term temperature curve at Koko Head (Figure 1B) one might conclude that interannual changes in environmental processes are unimportant. The Koko Head salinity curve (Figure 2B) shows such an inference to be incorrect and illustrates the value of monitoring more than one property at a location.

An understanding of the processes governing the temperature and salinity changes is pertinent to fishery management problems. Our speculations about these processes illustrate that good correlations between environmental properties and biological concentrations do not necessarily imply causal relationships. An example is the good correlation between skipjack tuna captures in the eastern Pacific yellowfin tuna regulatory area and central equatorial Pacific temperatures or the southern oscillation index, the skipjack tuna catches lagging about 18 mo.[5] Do these correlations mean that temperatures in the central equatorial Pacific determine larval survival and year-class strength or do they mean that the currents affect the concentration and distribution of skipjack tuna in the eastern Pacific with the temperature variations being ancillary? These questions are important if environmental factors are to be included in fishery population models.

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APPENDIX A

Sea-surface temperatures and salinities, Koko Head, Oahu, 1970-73: Phase angles and coefficients for harmonic functions.

$$S = K + bt + \sum_{n=1}^{h} C_n \cos \omega(nt - \alpha_n),$$

$$\omega = \frac{2\pi}{365} \text{ days}^{-1},$$

t is the time in days beginning with the first day in each year.

APPENDIX A TABLE 1.—Phase angles and coefficients for sea-surface temperatures, Koko Head, 1970-73.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	72.20	-80.01	52.33	38.44	81.41	50.88	-77.02	18.41	-89.79	85.22	-52.91	74.02	-84.68
1971	62.89	31.68	3.24	22.53	71.72	32.74	66.98	3.50	-10.93	-7.10	87.40	-80.98	-74.60
1972	62.93	21.24	68.54	-63.91	64.06	-70.46	83.06	-57.87	-48.34	-43.74	-8.51	76.71	24.69
1973	72.41	-4.17	-88.28	-59.54	-32.96	-89.25	-83.30	-50.69	57.26	-41.10	-19.01	-74.37	80.19

AMPLITUDES

	N-VALUES														
YEAR	K	B	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	25.5140	-0.0039	-1.8222	0.3590	-0.0552	-0.1421	-0.1264	-0.0868	0.1389	-0.1037	0.0876	-0.0646	0.0463	0.0780	0.0461
1971	24.7393	-0.0014	-1.3848	-0.3917	-0.1076	-0.1512	-0.1155	0.0318	-0.0722	0.0299	-0.1358	0.0295	0.0181	-0.0085	-0.0198
1972	24.4534	0.0003	-1.7160	-0.2903	0.0787	-0.1542	0.1731	-0.0360	-0.0577	0.0270	-0.0318	-0.0655	-0.0336	-0.0226	0.0417
1973	23.7849	0.0036	-1.0235	-0.0600	-0.1372	-0.1433	-0.1347	-0.0319	-0.0484	0.0860	0.0569	-0.0463	-0.0632	0.0468	0.0724

APPENDIX A TABLE 2.—Phase angles and coefficients for sea-surface salinities, Koko Head, 1970-73.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	75.16	-60.43	16.34	70.03	35.34	30.83	-37.70	-38.82	-26.93	-46.86	-77.26	21.73	-2.76
1971	-51.94	-80.21	-63.27	24.14	-45.10	-73.97	60.91	76.63	-34.16	-67.62	-14.74	36.53	-53.75
1972	9.27	-51.54	-89.46	-72.61	-11.74	-20.48	61.79	78.55	59.38	84.94	10.15	24.89	-24.50
1973	-82.26	88.25	23.40	-17.29	1.01	-27.39	-65.68	-60.90	37.04	90.17	-3.22	-50.96	2.98

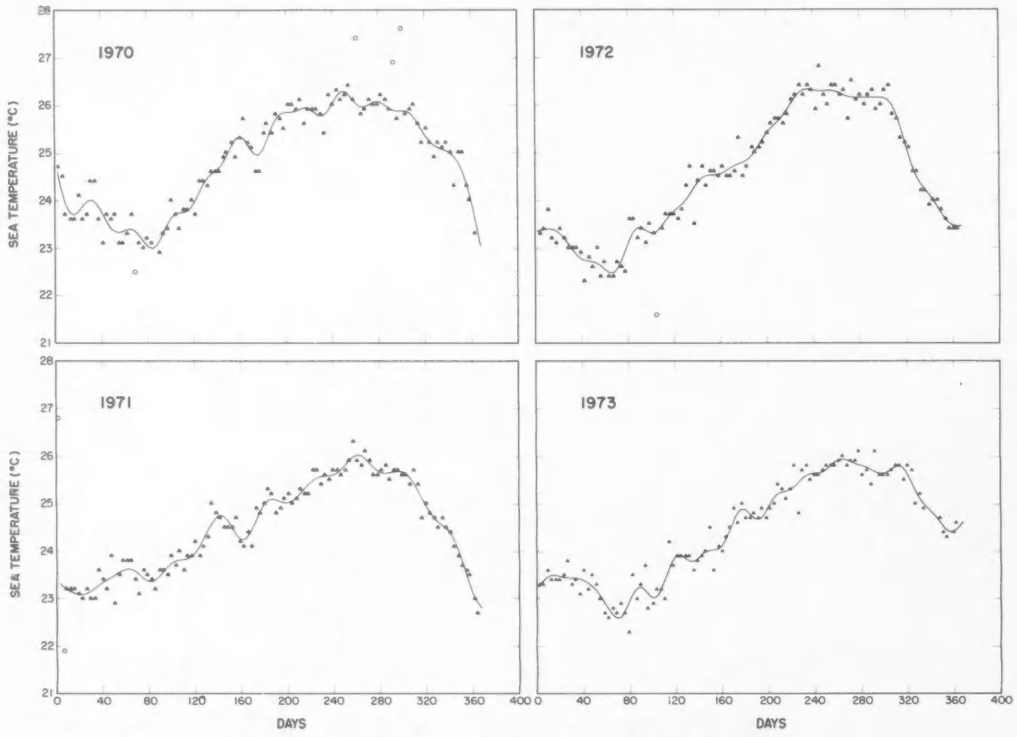
AMPLITUDES

	N-VALUES														
YEAR	K	B	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	34.8321	0.0009	0.0691	-0.0482	-0.0141	0.0196	0.0353	0.0107	-0.0073	0.0024	0.0002	0.0033	0.0059	-0.0115	-0.0105
1971	35.0025	0.0002	0.1115	-0.0132	0.0050	0.0111	-0.0078	0.0208	0.0160	-0.0036	0.0126	-0.0134	-0.0084	-0.0027	-0.0096
1972	34.9629	0.0	0.1838	-0.0807	0.0324	0.0365	0.0209	-0.0133	-0.0010	-0.0046	0.0127	0.0157	-0.0052	0.0089	-0.0085
1973	35.0231	-0.0002	0.0960	0.0213	0.0250	0.0341	0.0401	-0.0057	-0.0190	-0.0220	-0.0207	-0.0270	-0.0018	-0.0116	-0.0175

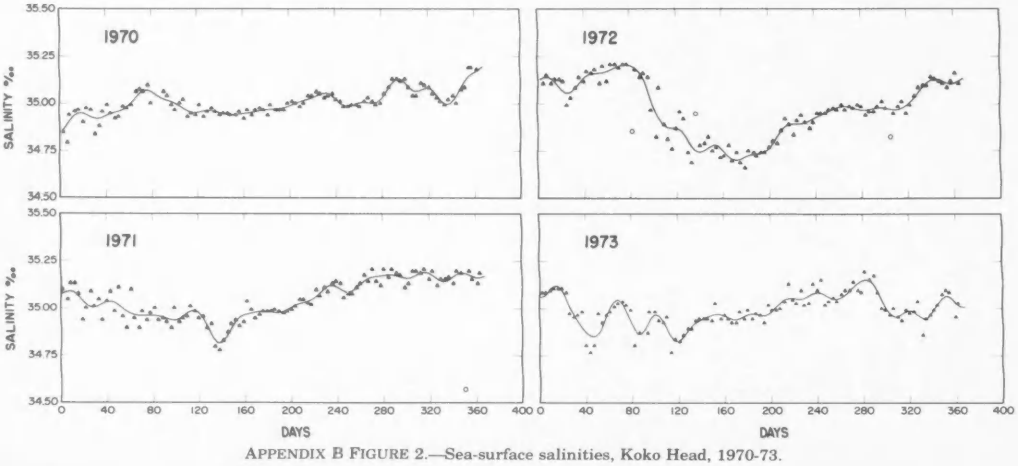
APPENDIX B

Sea-surface temperatures and salinities, Koko Head, Oahu, 1970-73: Fitted curves with observed values for each year.

Note: Circled observations have not been used in the harmonic analysis.



APPENDIX B FIGURE 1.—Sea-surface temperatures, Koko Head, 1970-73.



APPENDIX B FIGURE 2.—Sea-surface salinities, Koko Head, 1970-73.

APPENDIX C

Sea-surface temperatures, Christmas Island, 1970-73: Phase angles and coefficients for harmonic functions for each quarter of the year.

Days 1 to 120 = First quarter,
91 to 210 = Second quarter,
181 to 300 = Third quarter,
271 to 390 = Fourth quarter, extending 25 days into new year,

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n),$$

$$\omega = \frac{2\pi}{120} \text{ days}^{-1},$$

t is the time in days beginning with the first day of each quarter.

PHASE ANGLES IN DAYS

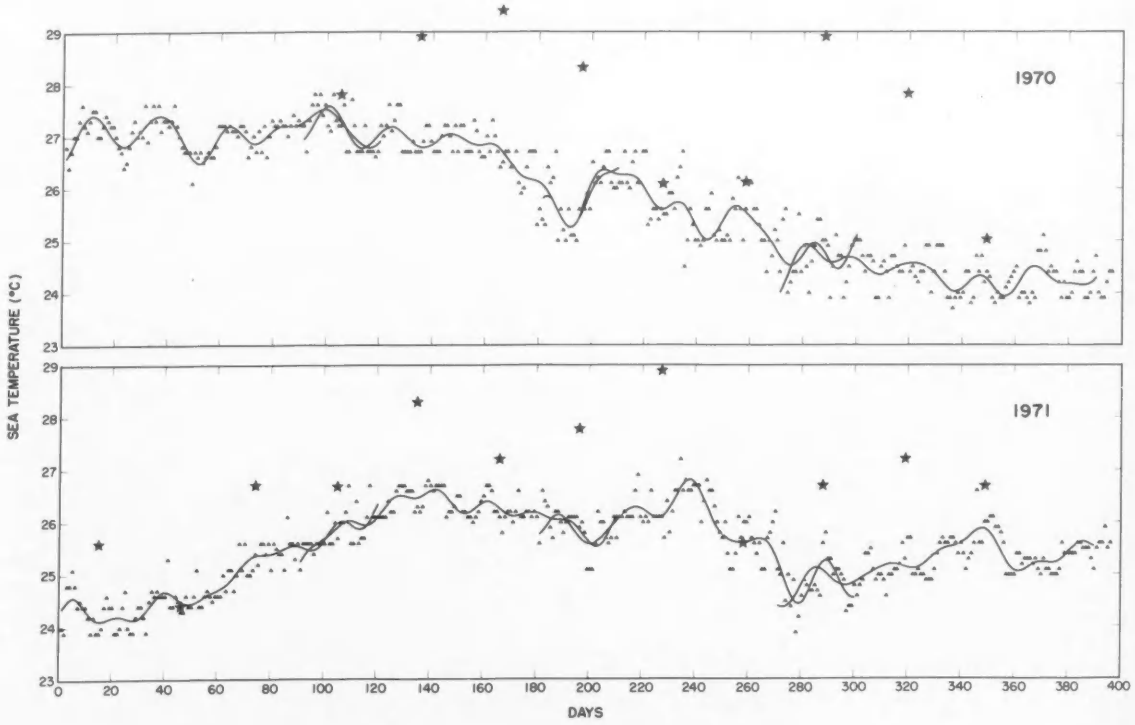
		N-VALUES						
YEAR	QU.	1	2	3	4	5	6	7
1970	1	12.44	-6.13	-16.78	-28.73	-2.08	6.81	16.58
	2	-22.81	17.61	7.60	14.33	0.98	13.05	-6.74
	3	-22.04	-10.25	-16.75	28.25	20.57	9.51	18.38
	4	26.63	-22.46	-18.15	-13.17	25.90	16.12	3.83
1971	1	-9.01	18.72	0.88	-23.22	-19.97	23.78	26.91
	2	-14.62	-11.07	-29.19	-19.30	18.78	-28.03	12.39
	3	-3.95	-4.74	8.40	-13.99	-2.60	-5.05	-20.05
	4	-7.34	24.95	-13.18	3.21	11.76	-16.66	25.18
1972	1	7.89	-27.53	-29.51	-14.94	-26.14	12.85	-22.64
	2	-7.77	-27.22	20.06	4.35	-1.33	21.18	19.69
	3	-6.13	-10.93	-15.60	29.25	28.38	21.23	18.53
	4	1.16	21.36	11.98	1.52	24.55	0.57	-19.27
1973	1	28.56	26.13	9.53	-4.76	-15.17	26.74	24.63
	2	28.96	21.19	12.08	25.17	-8.93	-29.78	-13.43
	3	23.99	-18.26	7.15	-11.40	-20.11	-13.58	16.48
	4	17.68	26.83	-28.88	27.12	-18.74	-21.21	18.01

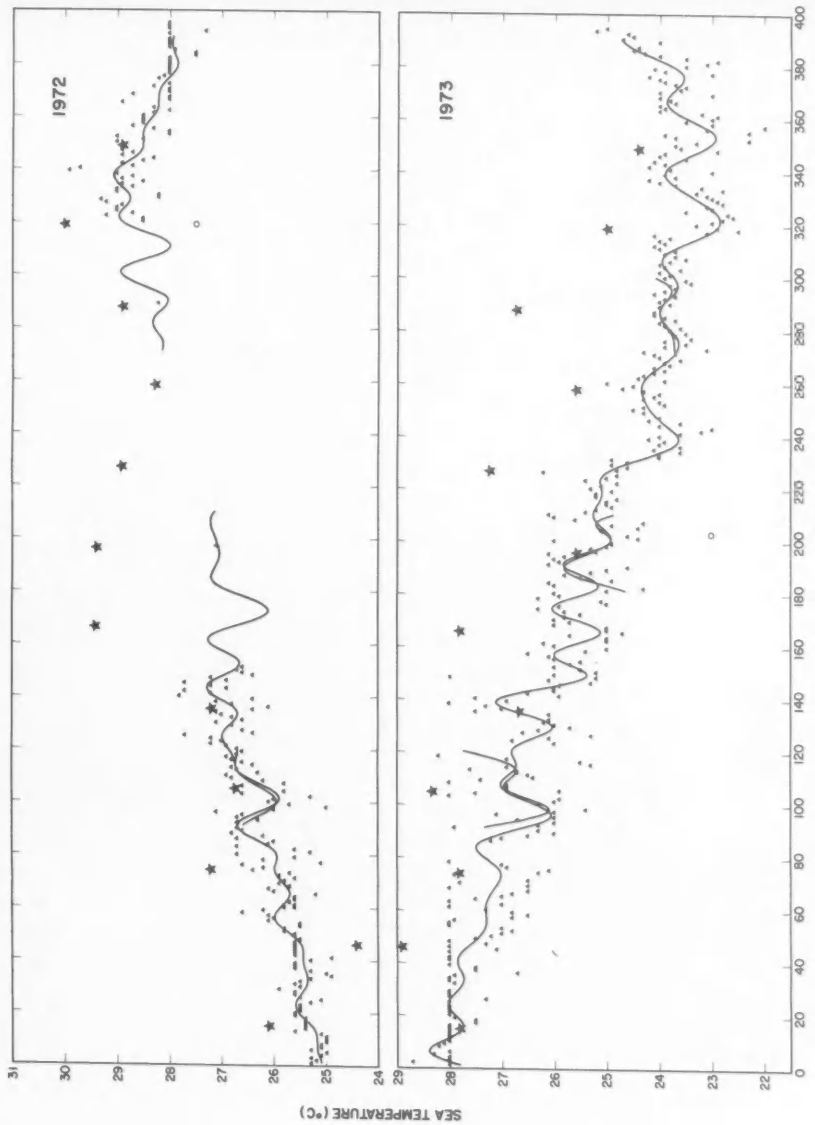
AMPLITUDES

				N-VALUES						
YEAR	QU.	K	B	1	2	3	4	5	6	7
1970	1	26.8641	0.0034	0.0851	-0.1983	-0.0753	-0.2552	-0.1641	0.0452	-0.0599
	2	26.8841	-0.0041	-0.4763	0.3681	0.1609	0.0824	-0.0936	-0.1511	-0.0466
	3	25.7091	-0.0049	-0.4564	-0.2126	0.1819	-0.0754	0.1993	0.0843	0.1694
	4	24.1813	0.0033	0.3638	-0.1038	-0.1890	-0.0981	0.1259	-0.0722	-0.0883
1971	1	23.9165	0.0176	0.1871	0.0905	0.1309	-0.1024	-0.0435	0.0735	0.1056
	2	25.6009	0.0083	-0.5389	-0.1219	-0.1488	-0.1029	0.0518	0.0146	0.0975
	3	25.3106	-0.0098	-0.5171	0.2021	0.0472	0.1281	-0.2729	-0.0450	-0.0912
	4	24.6692	0.0091	-0.2184	0.2117	0.0764	-0.1346	-0.0573	0.0837	-0.0717
1972	1	25.0308	0.0133	0.0496	-0.0682	-0.0819	0.1725	0.0891	-0.0318	-0.1120
	2	26.5641	0.0038	-0.1173	0.2415	-0.1913	0.0576	0.2075	-0.1676	0.1233
	3	27.3256	0.0120	-0.2914	-0.5543	0.5779	-0.2506	0.7281	-0.1929	-0.6557
	4	28.5913	-0.0019	-0.3996	0.1060	-0.1935	0.1134	0.1171	-0.1484	0.1384
1973	1	27.2621	0.0017	0.6704	0.3264	0.2433	0.0114	-0.1570	0.2590	0.0926
	2	27.3407	-0.0223	-0.1599	-0.3212	-0.0538	-0.2381	0.1734	-0.0976	0.3913
	3	24.6561	-0.0033	0.6202	-0.2669	0.2438	-0.2662	-0.1172	-0.1539	-0.0632
	4	23.0830	0.0092	0.5485	0.2358	0.1139	0.2976	0.1559	0.1038	0.0243

APPENDIX D

Sea-surface temperatures, Christmas Island, 1970-73: Fitted curves with observed values for each year. Circled observations have not been used in the harmonic analysis. Stars indicate values taken from *Fishing Information*.





APPENDIX D FIGURE 1.— Sea-surface temperatures, Christmas Island, 1970-73: Fitted curve with observed values for each year. Circled observations have not been used in the harmonic analysis. Stars indicate values taken from *Fishing Information* (see text footnote 3).

APPENDIX E

APPENDIX E TABLE 1.—Standard error of estimate (°C) for each annual temperature function at Koko Head, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

	n-values												
Year	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	0.41	0.32	0.32	0.30	0.29	0.28	0.26	0.25	0.24	0.24	0.23	0.22	0.22
1971	0.37	0.26	0.25	0.23	0.22	0.22	0.21	0.21	0.18	0.18	0.18	0.18	0.18
1972	0.35	0.29	0.28	0.26	0.23	0.23	0.22	0.22	0.22	0.22	0.21	0.21	0.21
1973	0.29	0.29	0.28	0.26	0.24	0.24	0.23	0.23	0.22	0.22	0.22	0.21	0.21

APPENDIX E TABLE 2.—Standard error of estimate (‰) for each annual salinity function at Koko Head, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

	n-values												
Year	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	0.055	0.043	0.042	0.040	0.031	0.030	0.029	0.029	0.029	0.029	0.029	0.027	0.026
1971	0.047	0.046	0.046	0.045	0.044	0.042	0.040	0.040	0.039	0.038	0.037	0.037	0.036
1972	0.080	0.058	0.054	0.047	0.044	0.043	0.043	0.043	0.042	0.041	0.040	0.040	0.040
1973	0.068	0.066	0.064	0.059	0.052	0.051	0.050	0.047	0.045	0.040	0.040	0.039	0.037

APPENDIX E TABLE 3.—Standard error of estimate (°C) for each quarterly temperature function at Christmas Island, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 7.

		n-values									*n*-values						
Year	Quarter	1	2	3	4	5	6	7	Year	Quarter	1	2	3	4	5	6	7
1970	1	0.35	0.32	0.31	0.25	0.23	0.22	0.22	1972	1	0.36	0.35	0.35	0.33	0.32	0.32	0.31
	2	0.46	0.37	0.35	0.35	0.34	0.32	0.32		2	Data sets incomplete or missing						
	3	0.50	0.47	0.46	0.45	0.43	0.43	0.42		3							
	4	0.39	0.38	0.36	0.35	0.34	0.33	0.33		4							
1971	1	0.30	0.30	0.28	0.27	0.27	0.27	0.26	1973	1	0.64	0.60	0.59	0.59	0.58	0.55	0.55
	2	0.30	0.29	0.27	0.26	0.25	0.25	0.24		2	0.71	0.68	0.69	0.66	0.65	0.64	0.58
	3	0.42	0.39	0.38	0.37	0.33	0.32	0.32		3	0.53	0.49	0.46	0.42	0.41	0.40	0.39
	4	0.34	0.31	0.30	0.29	0.28	0.28	0.27		4	0.46	0.43	0.43	0.37	0.35	0.34	0.34

APPENDIX F

Harmonic coefficients for the long-term series. Coefficients for each harmonic term in the series

$$S = a + bt + A_0 + \sum_n (A_n \cos n\omega t + B_n \sin n\omega t)$$

are given in the tables below. Harmonic analysis was performed on the residuals from a linear fit. If t is in months, for the Koko Head series, $\omega = \frac{2\pi}{216}$, and the first month in January 1956; for the Christmas Island series, $\omega = \frac{2\pi}{240}$, and the first month is January 1954.

APPENDIX F TABLE 1.—Coefficients for Koko Head temperature. $a = 23.7009$, $b = 0.0020$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	0.5478	−0.1755	−0.1397	0.1131	0.0279	−0.0538	0.0263	0.0583	−0.0782	−0.0245
10	0.0174	0.0760	−0.0642	0.0401	0.0905	0.0168	−0.0439	0.0641	−0.2483	−0.0055
20	0.1262	−0.0126	−0.0035	−0.0263	0.0408	−0.0211	−0.0253	−0.0235	0.0576	−0.0279
30	−0.0428	0.0019	−0.0060	0.0497	−0.0114	0.0191	−0.0134	−0.0348	−0.0041	−0.0258
40	0.0332	0.0042	−0.0024	−0.0502	0.0274	0.0056	0.0239	−0.0040	−0.0171	−0.0274
50	0.0377	−0.0436	0.0015	−0.0116	−0.1030	0.0298	0.0257	0.0154	−0.0007	0.0068
60	0.0162	−0.0113	−0.0050	−0.0267	0.0202	0.0202	0.0231	−0.0107	0.0145	−0.0234
70	−0.0174	0.0117	−0.0067							
					B_n					
0	—	0.0887	0.2135	0.1425	0.0305	0.0989	0.0023	0.0552	0.0418	0.0052
10	0.1329	0.0093	0.0696	0.0044	0.0437	−0.0274	0.0195	−0.0056	−1.4540	0.0197
20	0.0262	0.0509	0.0531	0.0198	0.0676	0.0572	−0.0049	0.0035	0.0105	−0.0409
30	−0.0313	0.0422	−0.0177	−0.0767	−0.0058	0.0373	−0.1468	−0.0175	0.0347	0.0226
40	0.0519	0.0306	0.0078	−0.0188	−0.0288	0.0258	0.0207	−0.0533	0.0105	−0.0327
50	0.0151	−0.0145	0.0652	−0.0230	−0.0113	−0.0283	−0.0074	0.0238	0.0050	0.0090
60	0.0188	−0.0138	0.0200	0.0272	−0.0316	−0.0222	0.0053	−0.0254	0.0177	−0.0083
70	0.0011	−0.0167	−0.0020							

APPENDIX F TABLE 2.—Coefficients for Koko Head salinity. $a = 35.0141$, $b = 0.0001$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	−0.1228	0.0366	0.0685	−0.0653	−0.0894	0.0441	−0.0034	−0.0048	0.0165	0.0163
10	0.0286	−0.0017	0.0109	−0.0128	−0.0156	0.0024	0.0043	0.0093	0.0903	−0.0020
20	−0.0004	−0.0095	0.0032	−0.0127	0.0017	−0.0035	0.0020	−0.0101	−0.0034	0.0028
30	0.0020	0.0117	−0.0043	−0.0097	−0.0132	−0.0023	−0.0091	0.0094	−0.0067	−0.0039
40	−0.0057	0.0085	0.0070	0.0040	−0.0136	−0.0098	−0.0035	0.0041	0.0030	−0.0053
50	−0.0031	−0.0062	0.0070	0.0130	−0.0002	−0.0092	−0.0053	−0.0002	0.0064	0.0046
60	−0.0006	−0.0048	−0.0039	−0.0021	0.0013	−0.0008	−0.0063	0.0002	0.0014	−0.0022
70	0.0089	−0.0016	0.0028							
					B_n					
0	—	0.0663	−0.0287	−0.0063	0.0206	0.0174	−0.0532	0.0026	−0.0221	0.0006
10	−0.0372	−0.0034	−0.0095	−0.0047	0.0268	−0.0041	0.0007	−0.0199	0.0085	0.0034
20	−0.0099	−0.0050	−0.0075	−0.0012	−0.0108	0.0029	0.0058	0.0075	0.0131	0.0026
30	0.0109	0.0028	0.0088	0.0086	−0.0105	−0.0095	0.0021	0.0126	0.0043	0.0138
40	−0.0050	−0.0067	−0.0039	0.0158	−0.0005	−0.0121	−0.0124	0.0064	0.0125	0.0092
50	−0.0002	0.0028	0.0037	0.0001	0.0050	0.0003	0.0001	−0.0089	−0.0003	−0.0000
60	0.0074	0.0108	−0.0071	−0.0070	0.0059	−0.0028	0.0028	0.0049	−0.0011	0.0007
70	0.0072	−0.0021	0.0015							

APPENDIX F TABLE 3.—Coefficients for Christmas Island temperature. $a = 26.1443$, $b = -0.0054$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	1.5694	−0.2024	−0.3409	−0.1310	0.1924	0.3505	−0.1455	−0.4605	−0.1400	−0.2839
10	0.1658	−0.3162	0.0228	−0.2507	−0.0381	0.1309	0.2614	0.0088	−0.0257	0.0569
20	−0.4204	−0.0517	−0.0635	0.0676	0.0431	0.0179	0.0014	−0.0727	−0.0298	−0.0637
30	0.0295	−0.0316	−0.0583	−0.0133	0.0264	0.0040	0.0073	−0.0021	−0.0587	−0.0397
40	0.1025	−0.0243	−0.0049	0.0496	−0.0108	0.0176	0.0054	−0.0458	0.0351	−0.0144
50	0.0100	0.0321	0.0211	−0.0272	0.0145	−0.0076	0.0085	0.0031	−0.0410	0.0141
60	0.0369	−0.0001	0.0292	−0.0495	−0.0385	−0.0080	−0.0065	0.0232	−0.0204	0.0170
70	0.0134	0.0126	−0.0021	−0.0141	0.0203	−0.0178	−0.0085	0.0325	0.0144	0.0445
80	0.0022									
					B_n					
0	—	−0.8028	−0.2146	−0.6457	−0.4963	−0.3942	−0.3880	0.1339	−0.1839	0.0969
10	−0.1253	0.1038	0.1556	−0.0039	0.0555	0.2400	0.1030	0.1198	−0.0589	0.1246
20	0.0883	0.0041	0.0403	−0.1501	−0.0233	0.0791	−0.0622	−0.0063	0.0252	0.0138
30	0.0456	0.0172	0.0133	−0.0420	−0.0357	0.0625	0.0097	0.0054	0.0347	−0.0026
40	−0.1791	−0.0090	0.0979	−0.0668	−0.0407	0.0247	0.0003	−0.0241	0.0154	−0.0151
50	0.0073	0.0230	0.0144	0.0196	−0.0277	−0.0250	0.0374	−0.0110	0.0054	0.0258
60	−0.0250	0.0336	−0.0219	−0.0223	−0.0124	−0.0314	0.0035	−0.0044	0.0041	0.0267
70	−0.0323	0.0071	−0.0183	−0.0084	0.0289	−0.0417	0.0431	−0.0055	0.0038	0.0022
80	0.0022									

A NEW GENUS AND SPECIES OF EELPOUT (PISCES, ZOARCIDAE) FROM THE GULF OF MEXICO[1]

HUGH H. DEWITT[2]

ABSTRACT

Exechodontes daidaleus n.gen. and n.sp., captured at lat. 27°01'N, long. 84°55'W at a depth of 503 m in the Gulf of Mexico, is described and figured. Its characteristics include the presence of pelvic fins, the absence of scales, teeth on the vomer but not on the palatines, the absence of enlarged canine teeth, teeth on the lateral margin of the dentary and directed outward, grooves behind the upper and lower lips interrupted at the symphyses, the absence of cephalic lateral-line pores, and a greatly reduced lateral line. The new genus appears to be most closely related to the Hadropareinae of the western North Pacific. A key to the genera of the Hadropareinae, including *Exechodontes*, is given.

During June of 1969 the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) RV *Oregon II* was engaged in a survey of shrimp abundance in relatively deep water (360-900 m) in the eastern Gulf of Mexico. Among the fishes captured is one small specimen of a zoarcid which does not appear to belong in any of the currently recognized genera of the family. More surprising, it seems most similar to a group of genera known only from the western North Pacific Ocean.

Exechodontes n.gen.

Type-Species *Exechodontes daidaleus* n.sp.

Diagnosis.—A zoarcid with pelvic fins and lacking scales, with vomerine teeth (two in type-species), but without palatine teeth. No enlarged canine teeth although a few anterior teeth in upper jaw somewhat enlarged; teeth of lower jaw small, in two distinct rows, the outer on the lateral and anterior edge of the dentary such that the teeth are directed outward and are visible when the mouth is closed. Grooves behind upper and lower lips interrupted at symphyses; upper lips not greatly broadened posteriorly. Pores of lateral-line canals absent on head and body; lateral line of body greatly reduced, only a few neuromasts visible close behind head and base of pectoral fin. Head small and without prominent bulging cheek musculature. Pelvic rays long, but only about distal one-fifth of their length bends to extend into the visible fins, the proximal four-fifths lying hidden beneath skin of ventrum. Branchiostegal rays six. Vertebrae with anterior and posterior halves of equal size.

Discussion.—Using various keys to the genera of Zoarcidae (Soldatov and Lindberg 1930; Norman 1966; Lindberg and Krasyukova 1975), *Exechodontes* falls into a group of three genera known only from the western North Pacific Ocean: *Hadropareia* Shmidt (1904) and *Bilabria* Schmidt (1936), both monotypic, and *Davidijordania* Popov (1931) with five species. These three genera constitute the subfamily Hadropareinae (Shmidt 1950), characterized by the absence of spines in the posterior portion of the dorsal fin, the presence of pelvic fins and the absence of crests on the chin (Lindberg and Krasyukova 1975). *Exechodontes* seems closest to *Hadropareia* in that it lacks scales and palatine teeth. *Hadropareia* has, however, distinct pores in the infraorbital lateral-line canal (other pores have not been described or illustrated) and a few pores in the anterior portion of the lateral line which extends posteriorly about three-fourths the length of the body. In addition, *Hadropareia* is described and figured as having the cheek musculature enlarged such that each cheek forms a prominent bulge (Soldatov and Lindberg 1930). *Davidijordania* differs from *Exechodontes* in having scales, palatine teeth and the groove behind the upper lip complete across the snout. *Bilabria* differs in having scales, pores

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in both the cephalic lateral-line system and the anterior part of the lateral line, and the lips of both jaws expanded (Soldatov 1922; Schmidt 1936; Shmidt 1950).

It is possible that the similarities described above are not of real phyletic significance. A. P. Andriyashev (pers. commun.) has pointed out that the Hadropareinae and some other genera (e.g., *Zoarces*) have vertebral centra with the anterior cone shorter than the posterior cone, i.e., the constriction of each amphicoelous centrum is shifted anteriorly. He adds that the Lycodinae, Lycogramminae, and Lycodapodidae have "symmetrical" centra with the constriction placed midway in the length of each centrum. The centra in *Exechodontes* are symmetrical, indicating that relationships may not be with the Hadropareinae (see Figure 3). I have, however, examined radiographs of *Macrozoarces americanus* and *Lycenchelys verrilli* and find that both have "asymmetrical" centra, at least anteriorly. Further analysis of vertebral characters seem indicated.

The following key should serve to separate the four hadroparein genera.

KEY TO THE HADROPAREINAE

1a. Cephalic lateral-line system without pores; outer teeth of lower jaw placed on anterior and lateral margins of dentary and directed outward; scales and palatine teeth absent ..... *Exechodontes* n.gen.

1b. Pores of cephalic lateral-line system present on upper parts of head; no outwardly directed teeth on lower jaw; scales and palatine teeth present or absent 2

2a. Scales absent; musculature of cheek enlarged, forming a prominent bulge along margin of preopercle; palatine teeth absent ..... *Hadropareia*

2b. Scales present; cheek musculature may be slightly swollen, but not forming a prominent bulge; palatine teeth present or absent 3

3a. Palatine teeth present; groove behind upper lip continuous across snout..... *Davidijordania*

3b. Palatine teeth absent; groove behind upper lip interrupted at tip of snout.. ..... *Bilabria*

Discovery of a zoarcid in the Gulf of Mexico that has its closest apparent affinities with a small group of genera in the northwestern Pacific is of zoogeographic interest. It is consistent with current thoughts regarding the origin and relationships of several faunal groups of the cooler North Atlantic which also have affinities with the North Pacific. The boreal North Pacific is considered a dominant evolutionary center which provided significant numbers of migrants that invaded the Arctic and North Atlantic during the late Miocene and late Pliocene epochs (Briggs 1974).

Discovery of *Exechodontes* might suggest that there are a number of undescribed species of the family inhabiting the slope waters of the American warm-temperate and tropical Atlantic. The only previously known zoarcid from the Gulf of Mexico is *Lycenchelys bullisi* Cohen which appears to be related to species found in the northern Atlantic and Gulf of Panama (Cohen 1964). Otherwise, the southernmost record for the family in the western North Atlantic is that of *Lycodes brunneus* Fowler from off the east coast of Florida just north of the Bahama Islands (Fowler 1944). In the eastern Atlantic, the family is known south to about lat. 20°N, where two species, probably both misidentified, have been captured at depths between 1,000 and 1,500 m (Vaillant 1888). The pelagic species *Melanostigma atlanticum* has been recorded southward only to the waters off Virginia (McAllister and Rees 1964). It is significant in the present context that *M. atlanticum* is most closely related to the western North Pacific *M. orientale* rather than the eastern North Pacific *M. pammelas* (Tominaga 1971).

Name.—From the Greek *exeches*, projecting, and *odontos*, teeth. The compound is a masculine noun.

Exechodontes daidaleus n.sp.

Holotype.—96.3 mm SL (standard length), collected at *Oregon II* station 10632: 27°01′N, 84°55′W, about 120 n.mi. ESE of Tampa Bay, Fla., in 503 m (275 fm); 124-ft shrimp trawl, dragged on the bottom, 18 June 1969. The specimen (Figure 1) has been deposited in the National Museum of Natural History, Washington, D.C., USNM 211797.

Description.—All measurements are given as

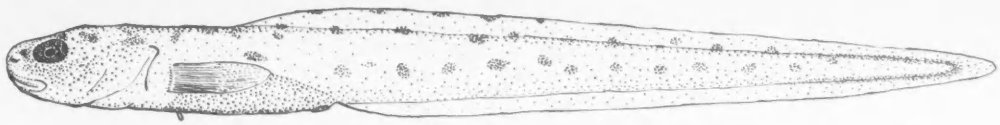

FIGURE 1.—Lateral view of holotype of *Exechodontes daidaleus* n.gen. and n.sp., USNM 211797, 96.3 mm SL.

thousandths of standard length unless otherwise indicated.

Head relatively short, 143 of SL, slightly compressed, its depth and width at cheeks, 78 and 69 of SL. Snout slightly greater than diameter of eye, 39 of SL, very bluntly rounded in both dorsal and lateral views. Nostrils 21 from tip of snout and eye, 36 apart, all of SL, placed at lateral edges of slightly bulbous median part of snout. Eyes placed high on head, but not bulging into dorsal profile, their diameter 34 of SL, placed 38 of SL apart (bony interorbit about 18 of SL). Postorbital part of head 76 of SL. Gill slit moderate, extending ventrally almost to lower edge of base of pectoral fin.

Gape of mouth relatively short, maxilla extending posteriorly to below anterior edge of pupil, length of upper jaw 57 of SL. Teeth all relatively small; those of upper jaw in a single, irregularly spaced row, a few teeth in anterior one third of jaw somewhat enlarged, especially adjacent to symphysis. Teeth of lower jaw in two distinct rows; inner row on dorsal edge of dentary, teeth somewhat irregularly spaced, none enlarged; outer row on lateral and anterior edge of dentary such that teeth are directed outward (most teeth in outer row are missing; cavities in dentary indicate probable tooth positions). Lower jaw included in upper, leaving anterior teeth of upper jaw and outer row of lower jaw visible when mouth is closed. Vomer with two teeth (one missing, but a large tooth cavity present); palatines edentulous. Gill rakers of anterior series of first arch 0 + 0 + 12; those of posterior series 0 + 0 + 11; all are short and blunt. About nine small nubbins present in posterior series of last arch. Pseudobranchiae absent.

Grooves behind lips of both jaws interrupted at symphyses; upper jaw appears to be nonprotractile. Lips narrow, not expanded. No fleshy protuberances or crests present on lower jaw; no cephalic lateral-line pores present anywhere on head (Figures 1, 2). Oral valves present in both jaws, that of lower jaw appearing double, one thin and membranous, lying somewhat anterior and overlying a more fleshy one. Tongue fleshy. Branchiostegal rays six on both sides.

Body slender and compressed, its depth and width 78 and 48 of SL; pectoral to pectoral distance 71 of SL. Lateral line not prominent; a single, prominent, raised neuromast present on each side just above and slightly anterior to upper end of gill slit; a few similar organs (appearing as pale spots) visible in a line curving downwards toward midline behind pectoral fin. Skin delicate but firm on the body. Scales absent. Vertebrae 19 + 78 = 97 (including urostylar vertebra). Vertebrae appear in radiographs to be amphicoelous with anterior and posterior cones of equal size (Figure 3).

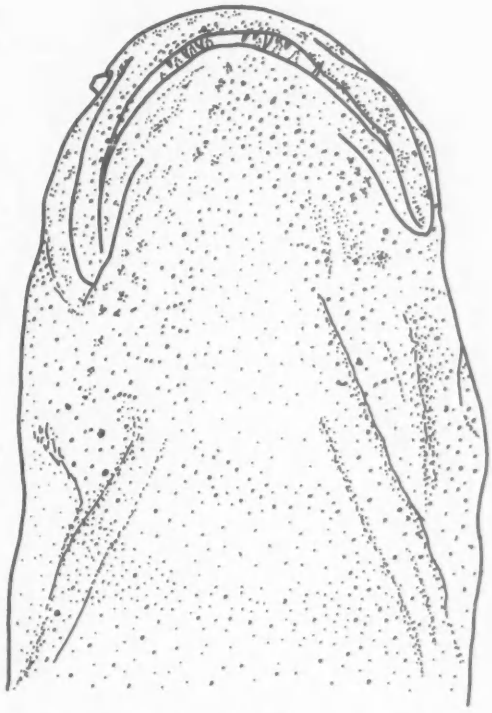

FIGURE 2.—Ventral view of head of holotype of *Exechodontes daidaleus* n.gen. and n.sp., USNM 211797, 96.3 mm SL. Missing teeth in outer row of lower jaw outlined in dots to show presumed position and size.

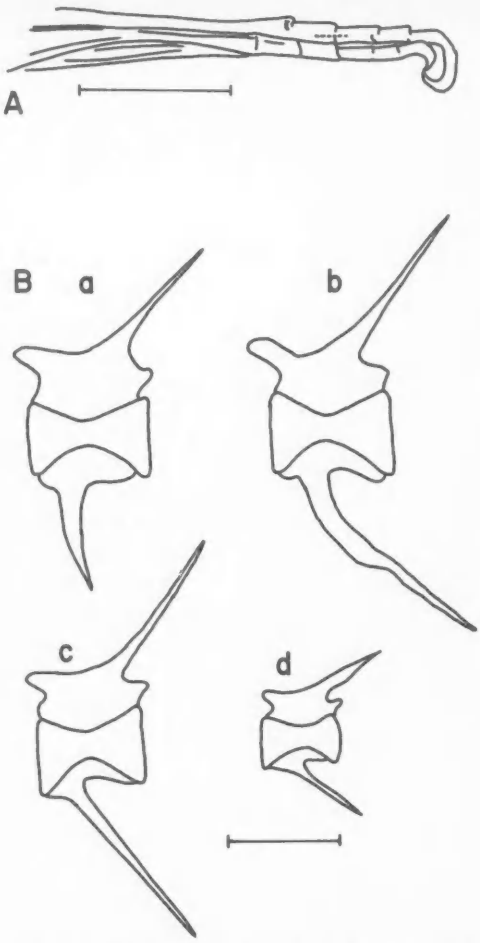

FIGURE 3.—Holotype of *Exechodontes daidaleus* n.gen. and n.sp., USNM 211797. A. Left pelvic rays; the tips originally were straight at about a right angle to main axis. B. Outlines of selected vertebrae traced from a radiograph with the aid of a camera lucida: a, vertebra no. 14; b. no. 20; c, no. 50; d, no. 80. The lines equal 1 mm.

Upper part of small intestine greatly enlarged, about equal in volume to empty stomach. Two very blunt, short and broad pyloric caeca just posterior to thick and muscular pylorus. Gallbladder large and transparent, lying between liver and enlarged upper intestine. A pair of thin gonad chords extending from midway in length of body cavity almost to anus indicate holotype is a male.

Pectoral fins with 15 rays, rounded in outline when rays spread, their length and width of base 104 and 27 of SL, not reaching to above anus. Pelvic fins with two rays, appearing as a pair of small nipples below and slightly behind bases of pectoral fins, their length about 6 of SL. The rays, however, are much longer, 31 of SL, originating anterior to the pectoral fins and lying for most of their length horizontally beneath the skin with only their distal ends bent sharply into the visible nubbins (Figure 3).

Dorsal fin originates behind bases of pectoral fins, above about middle of their length, 235 of SL from tip of snout and 786 from base of caudal fin, with 86 rays. Anal fin originates below base of 12th ray of dorsal fin 341 of SL from tip of snout, 683 of SL from base of caudal fin, and 215 of SL from nipples of pelvic fins, with 79 rays. Caudal fin 38 of SL, with a total of about eight rays.

Color (in alcohol) very pale yellow-brown, almost white, with large, scattered brown melanophores, especially over ventral two-thirds of body which is therefore slightly darker than upper one-third. Small to medium-sized (about 1-3 mm in diameter), irregularly shaped and placed brown spots on upper half of body, rather widely spaced (separated by at least their own diameter). Cheeks and snout darker than body, with more numerous melanophores; brown pigment present in an arc around front of eyes; tip of snout brown. Lower jaw with darker areas of larger and more numerous melanophores. Darker pigment present along bases of posterior parts of dorsal and anal fins, and base of caudal fin. Pelvic nipples brown; pectoral fins with brown pigment. Peritoneum very dark brown, showing through belly as dark blue-grey; viscera pale. Lining of mouth and pharynx pale. Anus ringed with black.

Name.—From the Greek *daidaleos,* dappled or spotted.

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Museum of Natural History very kindly permitted me to examine zoarcid material from the western North Pacific in their care, provided space and facilities for work, and helped in obtaining literature on western Pacific zoarcids.

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SEASONAL MIGRATION OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, INTO NORTH AMERICAN COASTAL WATERS: DISTRIBUTION, RELATIVE ABUNDANCE, AND ASSOCIATION WITH TRANSITION ZONE WATERS

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ABSTRACT

In the spring months of 1972-74, fishery-oceanography surveys were conducted in the eastern North Pacific which combined intensive oceanographic sampling by research vessels with concurrent fishing effort for albacore by chartered commercial fishing vessels. The catches demonstrate an association of albacore distribution with the Transition Zone and its boundaries. The relative abundance of albacore was found to be high in the eastern sector of the Transition Zone or a period just prior to their movement across the California Current and into the traditional nearshore fishing grounds. These centers of high relative abundance of albacore are sometimes sufficient to support commercial fishing earlier and farther offshore than the traditional fishing season. Variations in the pattern of migration occur in apparent response to variations in the character and development of the Transition Zone and its frontal structure. Analyses of albacore tagging and size frequency data provide evidence that the shoreward-migrating albacore of the Pacific Northwest and California are independent groups.

The North Pacific albacore, *Thunnus alalunga* (Bonnaterre), is a wide-ranging species which spawns in the central subtropical Pacific, performs transpacific migrations, and supports important commercial fisheries in the western, central, and eastern North Pacific. That marked variations in distribution and relative abundance of albacore occur in the eastern North Pacific is indicated by major latitudinal shifts in the location of the U.S. fishery off the west coast of North America (Laurs et al. 1976). In order to evaluate factors which may affect variations in distribution, relative abundance, and migration patterns of albacore in the eastern North Pacific, and to improve our understanding of the underlying factors affecting the onset and subsequent development of the fishery, early season surveys were conducted in offshore waters of the North American Pacific coast in 1972-74.[2] These surveys found that relative abundance of albacore was high in the vicinity of oceanic fronts of the Transition Zone waters in the eastern North Pacific. Survey results also provide the basis for a hypothesis concerning migration of albacore into coastal waters off the west coast of North America. During these surveys albacore were taken in commercial concentrations farther offshore than traditionally, and several weeks earlier than the fishing season which usually commences in mid-July.

BACKGROUND INFORMATION

Numerous exploratory albacore fishing and albacore oceanographic surveys have been conducted in the central and eastern North Pacific. From surveys conducted during the 1950's, scientists described seasonal variations in distribution of albacore in the central and parts of the eastern Pacific, and demonstrated the association of albacore with Transition Zone waters in the central North Pacific (Shomura and Otsu 1956; Graham 1957; McGary et al. 1961). Flittner (1963, 1964) reported on albacore trolling experiments conducted from U.S. Navy picket vessels operating approximately along long. 130° to 135°W, and presented a schematic model of albacore movement off the Pacific coast (Flittner 1963). Neave and Hanavan (1960) showed that the northern limit of albacore catches made during high-seas salmon gillnetting studies conducted between long. 125° and 175°W was about lat. 45° to 47°N in July and

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[2]These surveys were carried on cooperatively by the National Marine Fisheries Service, Southwest Fisheries Center La Jolla Laboratory, and the U.S. albacore fishing industry through the American Fishermen's Research Foundation.

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lat. 45° to 50°N in August and September. According to Brock (1943), yachts sailing between Hawaii and Oregon during June made albacore catches between lat. 30° and 44°N in waters between long. 154° and 140°W.

Numerous exploratory fishing and oceanographic surveys also have been conducted within a few hundred miles of the coast to obtain information on distribution, availability, and migration patterns of albacore during early season in waters off the Pacific Northwest (Powell 1950, 1957; Powell and Hildebrand 1950; Powell et al. 1952; Schaefers 1953; Owen 1968; Meehan and Hreha 1969; Pearcy and Mueller 1970; and others), and in waters off California (Graham 1959; Clemens 1961; Craig and Graham 1961; and others listed in Clemens 1961 and Pinkas 1963). Johnson (1962), Laurs et al. (1976), and others have discussed variations in distribution and relative abundance of albacore in waters off North America where the U.S. fishery takes place. These studies have shown: 1) the limits of where albacore are found; 2) their general migration patterns; 3) the importance of environmental conditions and changes, notably ocean temperature, in relation to the distribution and relative abundance of albacore; and 4) the considerable annual variation in location of available concentrations of albacore.

In the present study early season albacore surveys were planned to encompass a portion of the eastern sector of the Transition Zone during a period prior to the commencement of the nearshore fishery. The primary objectives of these surveys were:

1) To investigate the early season distribution and abundance of albacore off the North American Pacific coast.
2) To investigate the eastward migration path of albacore entering the American west coast fishery.
3) To determine if migrating albacore are associated with major offshore oceanographic features, particularly the Transition Zone and the ocean fronts that form its boundaries.

METHODS

The general work plan for each offshore survey employed one National Marine Fisheries Service (NMFS) research vessel (*Townsend Cromwell* in 1972 and *David Starr Jordan* in 1973 and 1974) and a group of 5 to 12 commercial albacore fishing vessels on charter to the American Fishermen's Research Foundation (AFRF). The research vessel and chartered fishing vessels worked cooperatively to obtain estimates of distribution and relative abundance of albacore in the offshore area and to make concurrent oceanographic measurements. The research vessel collected physical, chemical, and biological oceanographic data and conducted supplementary fishing activities. The fishing vessels conducted exploratory fishing, tagged fish, and collected surface and subsurface temperature data. The oceanographic findings made on meridional transects were used in directing the exploratory fishing operations, particularly at the onset of each survey. In several instances, especially in 1973 and 1974, the findings of large numbers of fish were used to redirect the research vessel to conduct detailed oceanographic observations in the vicinity.

Operations Aboard Research Vessels

Three meridional oceanographic sections were taken along long. 135°, 137°30′, and 140°W between lat. 31° and 41°N in 1972 and 1973; in 1974 the middle section, portions of the section along long. 135°W, and additional transects were taken (Figure 1). Hydrographic stations were occupied at 25- to 30-n.mi. intervals. Figure 2 shows station positions occupied in 1973; Lynn and Laurs[3,4] gave figures of the station positions for other years. Observations included: 1) salinity-temperature-depth profiles to 500 or 1,000 m using an STD;[5] 2) Nansen bottle or command rosette sampler[6] bottle casts for collection of water samples for determination of dissolved oxygen, chlorophyll, and salinity; 3) oblique zooplankton net hauls and simultaneous surface hauls with neuston plankton nets; and 4) at night stations,

[3]Lynn, R. J., and R. M. Laurs. 1972. Study of the offshore distribution and availability of albacore and the migration routes followed by albacore tuna into North American waters. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1972, p. 10-44. (Unpubl. rep.)

[4]Lynn, R. J., and R. M. Laurs. 1973. Further examination of the offshore distribution and availability of albacore and migration routes followed by albacore into North American waters. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1973, p. 3-35. (Unpubl. rep.)

[5]Plessey model 9006 electronic salinity-temperature-depth profiler. Use of a trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6]General Oceanics, Inc.

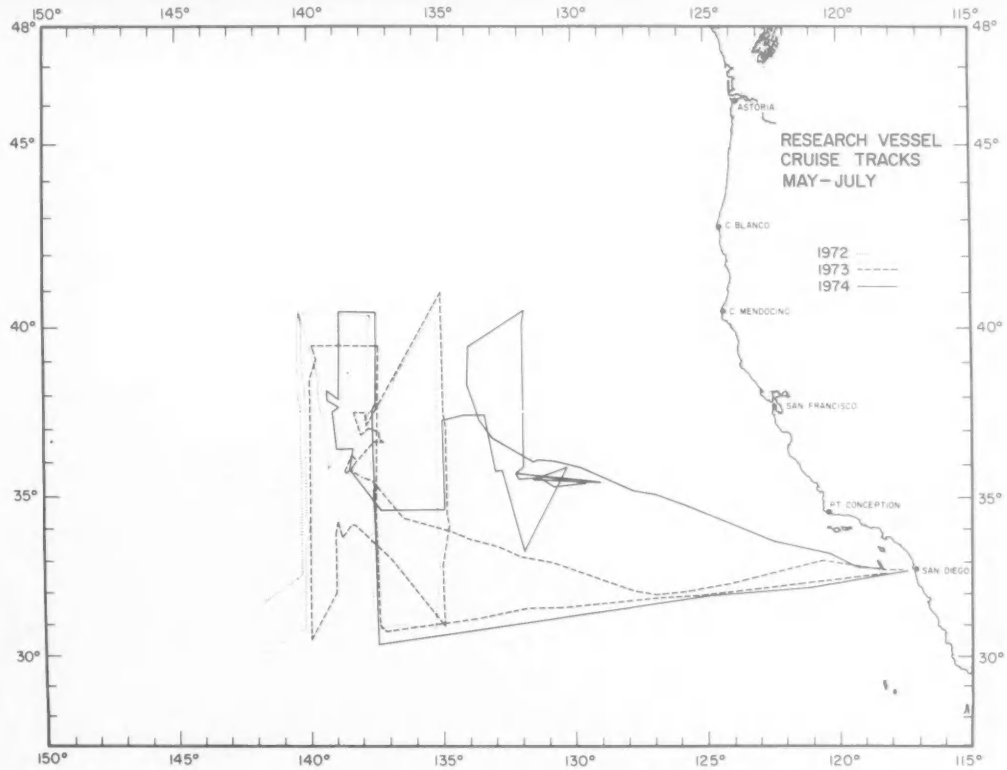


FIGURE 1.—Albacore research vessel cruise tracks for the 1972-74 offshore research surveys.

oblique midwater trawl hauls using an Isaacs-Kidd Midwater Trawl. Also, surface temperature, salinity, and chlorophyll were recorded continuously while underway.

Generally, 10 jiglines (five on *Townsend Cromwell* cruise in 1972) were trolled for albacore on transects between oceanographic stations during daylight. In some regions that were not covered by fishing vessels, trolling was carried on by the research vessel exclusively throughout daylight. On such fishing days, three or four expendable bathythermograph (XBT) drops were made in addition to continuous monitoring of surface temperature, salinity, and chlorophyll.

Operations Aboard Fishing Vessels

The AFRF charter vessels which took part in the offshore surveys were jigboats, except for two baitboats in 1973 which were outfitted to conduct either live-bait fishing or jig fishing. Twelve fishing vessels participated in the operations in 1972 and 1973 and five in 1974.

The fishing vessels sailed in groups of four from San Diego, Calif., and Astoria, Oreg., at 15- to 20-day intervals during 1972 and 1973, and all vessels sailed together from San Diego in 1974. The vessels usually worked in pairs. A schematic diagram of the cruise tracks for the 1972-74 offshore surveys is shown in Figure 3. Detailed cruise tracks showing daily positions and locations of XBT stations for each fishing vessel or pair of fishing vessels by 10-day period are given in Lynn and Laurs[7] (see footnotes 3 and 4).

[7]Lynn, R. J., and R. M. Laurs. 1974. Cooperative NMFS-AFRF early season offshore studies conducted during 1974. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1974, p. 3-18. Southwest Fish. Cent. Admin. Rep. LJ-74-47.

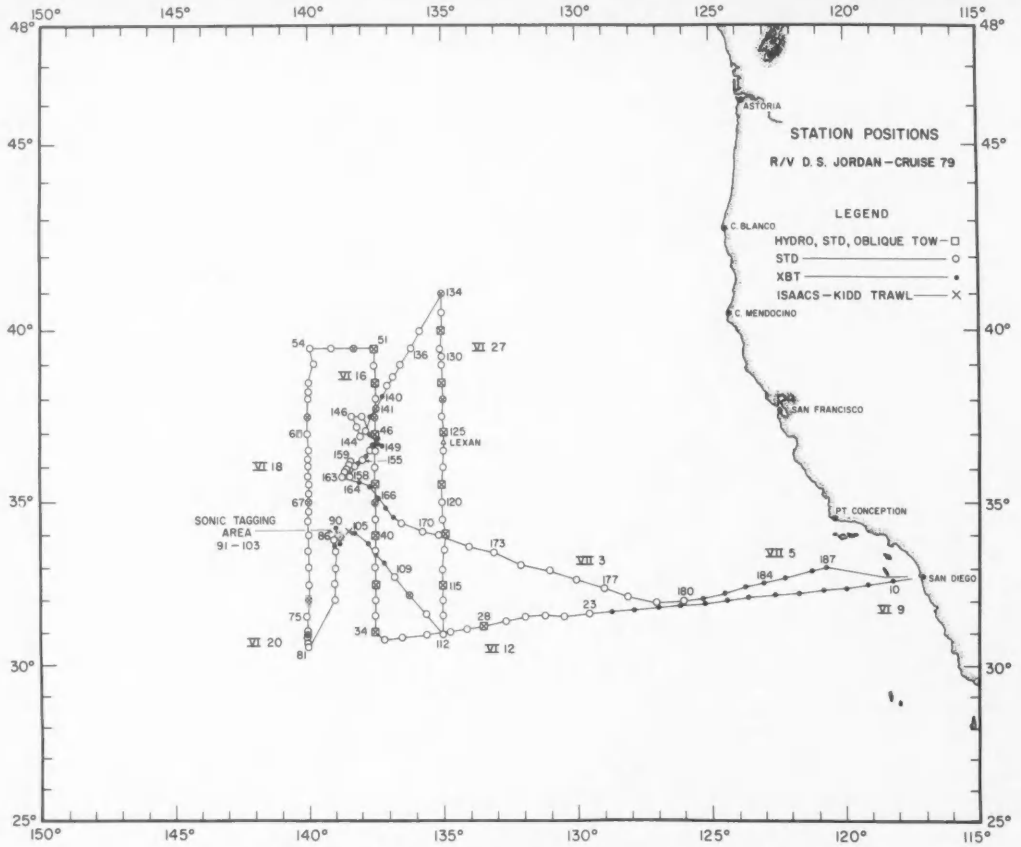


FIGURE 2.—Track and station positions for RV *David Starr Jordan* cruise 79, 9 June-6 July 1973.

Standard commercial albacore fishing equipment and regular commercial fishing methods were used. Most of the jig vessels trolled 10 lines and baitboats 6 or 8 lines when jig fishing. (Baitboats had better success when trolling than when baitfishing.) Daily records pertaining to fishing operations were maintained aboard each vessel, including number of fish caught, fork length of most fish caught (except for two vessels in 1972), positions where fishing was started and ended, amount of fishing effort expended, and fishing conditions and signs of fish. In addition, sea-surface temperature, sea conditions, and surface weather conditions were recorded. Half of the fishing vessels chartered in 1972 and 1973, and all in 1974, were equipped with an XBT system; generally one or two XBT probes were launched each day. Sea-surface temperature measurements were made using bucket thermometers.

EARLY SEASON DISTRIBUTION AND RELATIVE ABUNDANCE OF ALBACORE IN OFFSHORE WATERS

Distribution of Catches Made By Charter Vessels

Nearly 27,000 albacore were caught by the chartered fishing vessels during the three offshore surveys (Table 1). In all three surveys, albacore were taken in substantial numbers in an offshore region between lat. 31° and 36°N from late May through June. Catch rates were generally low or zero in surrounding regions and during explorato-

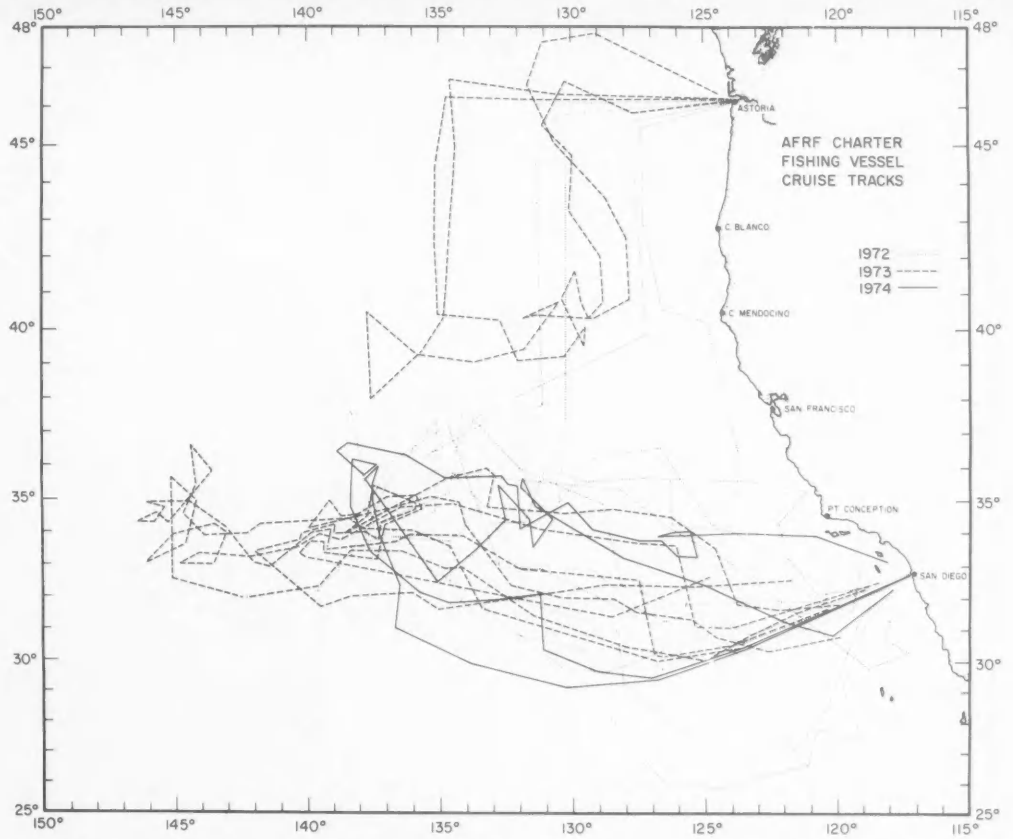


FIGURE 3.—American Fishermen's Research Foundation charter fishing vessel cruise tracks for the 1972-74 offshore research surveys.

ry fishing before late May. Variations in distribution and relative abundance of albacore were observed within and between surveys.

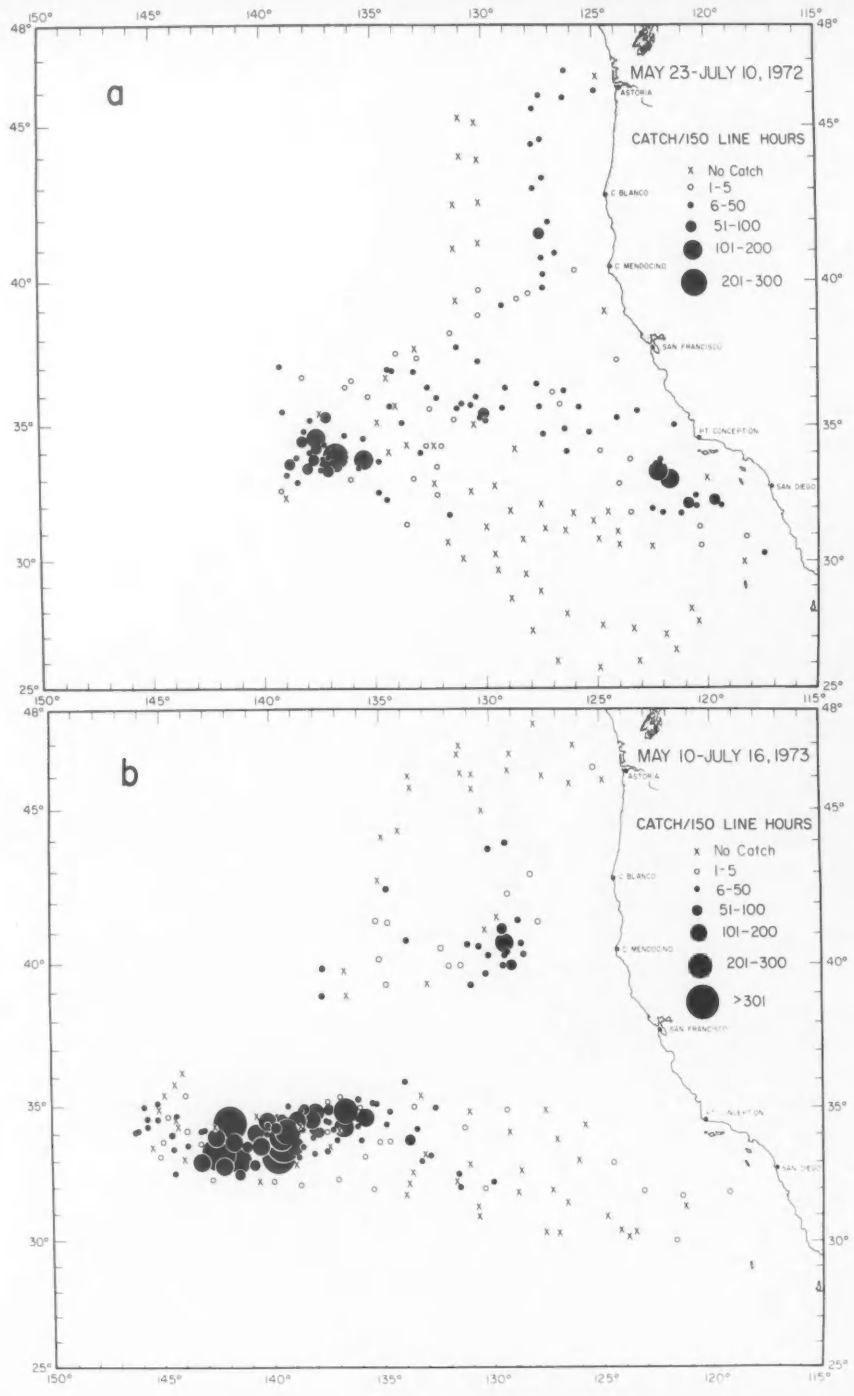
Differences Between Surveys

Plots of the charter vessel catches for each survey are given in Figures 4a-c. The catches represented in these and other plots have been standardized to the number of fish caught per 150 line-hours (averaged between pairs of vessels that fished together for 1972 and 1973) and presented graphically by proportionately increasing size of dots.

TABLE 1.—Albacore survey catches.

Year	Total catch by charter vessels	Tagged and released	Total catch by research vessel
1972	6,746	1,431	155
1973	11,027	1,738	130
1974	9,146	1,369	495
Total	26,919	4,538	780

In 1972 and 1973, relative abundance of albacore was high between lat. 32° and 35°N, long. 135° and 140°W, and lat. 32° and 35°N, long. 135° and 143°W, respectively (Figure 4a-b). In both of these years small or no catches were made in the region between long. 135°W and inshore waters within 150 mi of the coast where fishing takes place during the traditional albacore fishing season. In 1974 (Figure 4c), high catch rates were again made offshore of long. 135°W, but over a larger latitudinal range, lat. 31° to 36°N, and somewhat more scattered than in the two preceding years. Also, high catches were made at about lat. 33° to 36°N, long. 124° to 135°W in the region between


a
MAY 23-JULY 10, 1972
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
ASTORIA
C. BLANCO
C. MENDOCINO
SAN FRANCISCO
PT. CONCEPTION
SAN DIEGO
b
MAY 10-JULY 16, 1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°

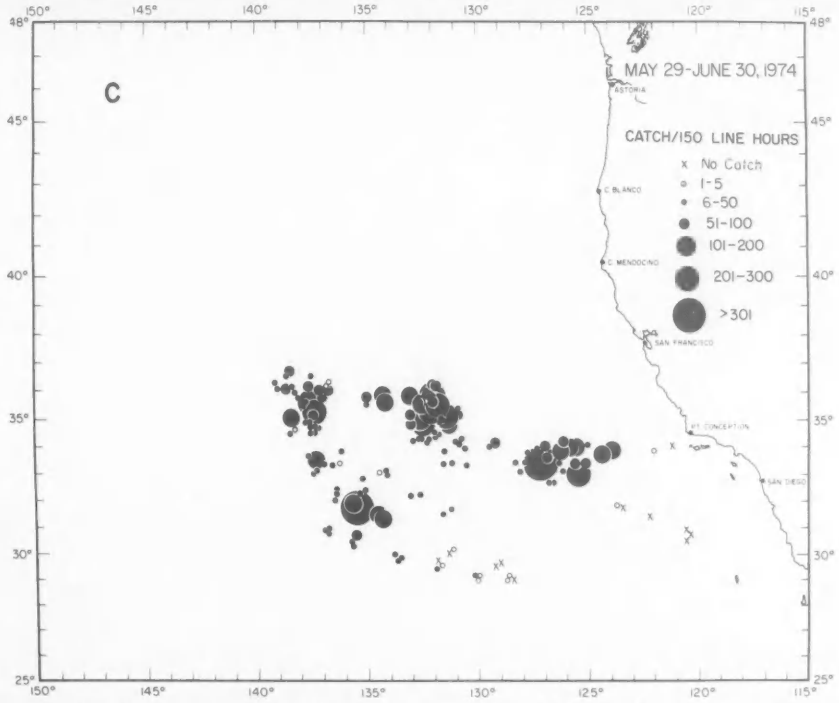
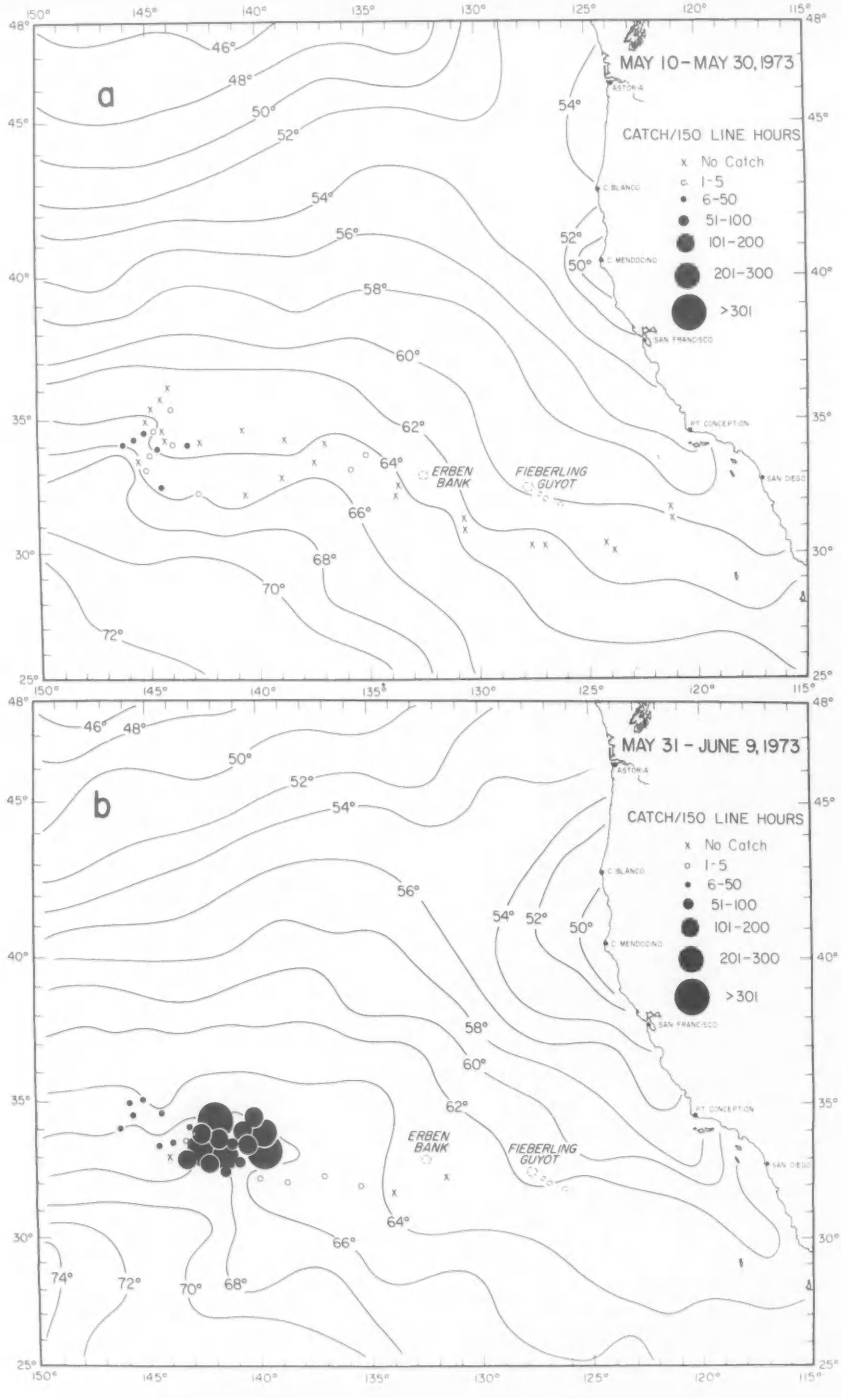


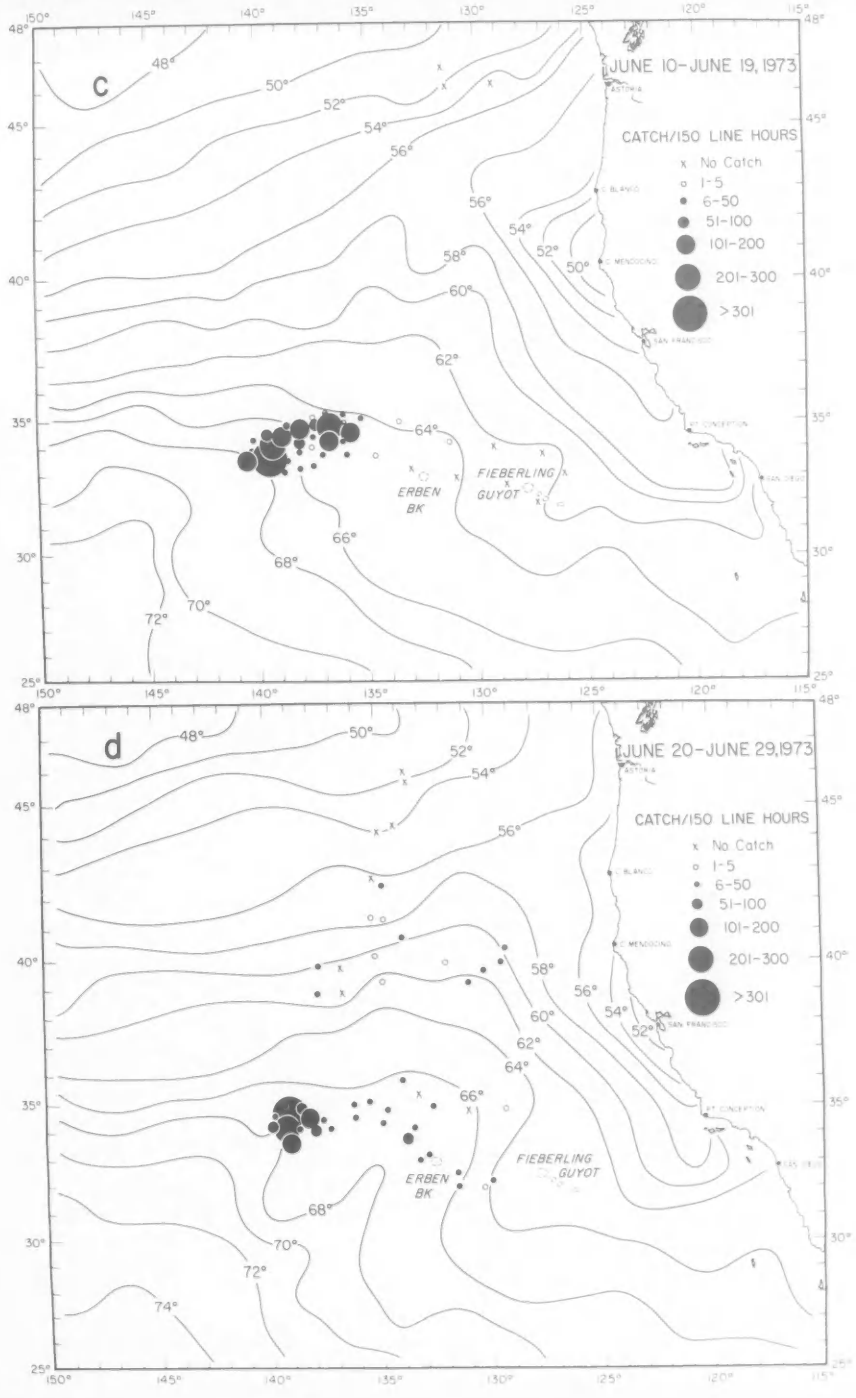
FIGURE 4.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels: a. 23 May-10 July 1972; b. 10 May-16 July 1973; c. 29 May-30 June 1974.

the offshore area of high catches and inshore waters.

Differences Within Surveys

Representative information on spatial and temporal variations in the distribution and relative abundance of albacore in offshore waters during May and June is given in Figure 5a-e. In the early part of the 1973 survey, 10 to 30 May, four vessels worked westward making only small scattered catches between lat. 31° and 35°N, long. 142° and 145°W. In the second time period, 31 May to 9 June, the vessels returned through waters they had scouted earlier and began making catches of over 100 fish/day between lat. 32° and 34°N, long. 139° and 143°W. Good catches continued to be made in the general area of lat. 33° to 35°N, long. 135° to 143°W for several weeks with charter vessels landing up to 300 fish/day on many days. A second group of four charter boats, which left San Diego on 25 May, did not catch any fish until 4 June when they moved westward of long. 139°W near lat. 33° to 35°N. On their return to San Diego during mid-June, the first group of boats failed to catch any fish east of long. 135°W despite favorable ocean temperature conditions. Similarly, on the return to San Diego near the end of June, catches by the second group of charter boats dropped off abruptly east of long. 135°W with only small scattered or no catches made east of Fieberling Guyot (long. 128°W). The four vessels surveying the area north of lat. 38°N found generally poor to moderate catches. (The region lat. 35° to 38°N was not covered by the fishing vessels.) This sequence of catch charts shows that: 1) albacore were apparently unavailable to jig fishing, except for scattered catches, through May in a region which subsequently was to prove very productive; 2) albacore became available to trolling gear in the first week of June in a region which will be shown later to be associated with the subtropic boundary of the Transition Zone; 3) good catches persisted within a block of 2° latitude by 7° longitude for


a
MAY 10 – MAY 30, 1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ASTORIA
C. BLANCO
C. MENDOCINO
SAN FRANCISCO
PT. CONCEPTION
SAN DIEGO
ERBEN BANK
FIEBERLING GUYOT
b
MAY 31 – JUNE 9, 1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ASTORIA
C. BLANCO
C. MENDOCINO
SAN FRANCISCO
PT. CONCEPTION
SAN DIEGO
ERBEN BANK
FIEBERLING GUYOT


c
JUNE 10–JUNE 19, 1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ERBEN BK
FIEBERLING GUYOT
d
JUNE 20–JUNE 29,1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ERBEN BK
FIEBERLING GUYOT

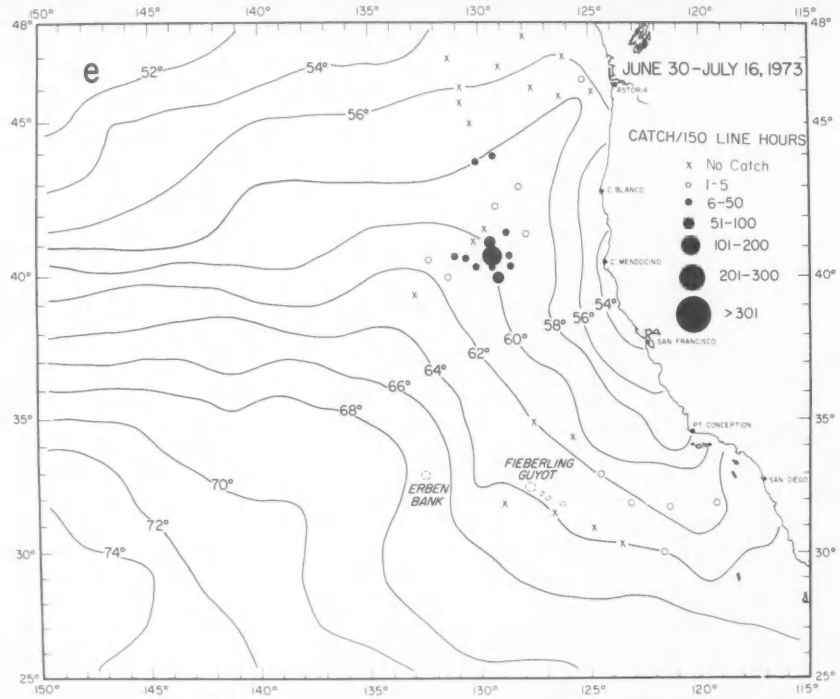


FIGURE 5.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels and sea-surface temperature: a. 10-30 May 1973; b. 31 May-9 June 1973; c. 10-19 June 1973; d. 20-29 June 1973; e. 30 June-16 July 1973.

over a 3-wk period in June, and 4) elsewhere catches were substantially lower.

Catches Made By Noncharter Commercial Fishing Vessels

Because of the fishing success of the chartered fishing vessels, in the years following the first survey (1972), noncharter commercial albacore vessels have fished in the offshore region concurrently with the chartered fishing vessels and research vessels. During June 1973 and June 1974 it is estimated that, respectively, 25 to 30 and 50 to 60 albacore vessels fished across a large zone of latitudes in the offshore regions (Jack Bowland pers. commun.). Additional information on the distribution and relative abundance of albacore is provided by these catch data.

Figure 6a-e shows estimates of mean catch-per-unit effort by 15-day period and 1° quadrangle of latitude and longitude for May through July 1973, for those commercial albacore vessels from which logbook records were available. [Logbook records were standardized by methods given in Laurs et al. (1976).]

As with the charter vessels, a center of high relative abundance was found in the offshore region between lat. 33° and 35°N and long. 139° and 143°W. From mid-May through mid-June (Figure 6a, b) no catches were reported north of lat. 36°N nor (with one exception) east of long. 134°W. In the latter half of June (Figure 6c), a scattering of catches was made in the intervening zone. The distribution and relative abundance of albacore, indicated by the charter and noncharter fishing vessel catches, were similar. Catches by noncharter vessels were made over the same latitudinal range and the same offshore to nearshore sequence was observed. The fishing success of the noncharter vessels further demonstrates that commercial concentrations of albacore were available 4 to 6 wk earlier than the normal fishing season in waters hundreds of miles offshore of the area where the fishery has traditionally operated.

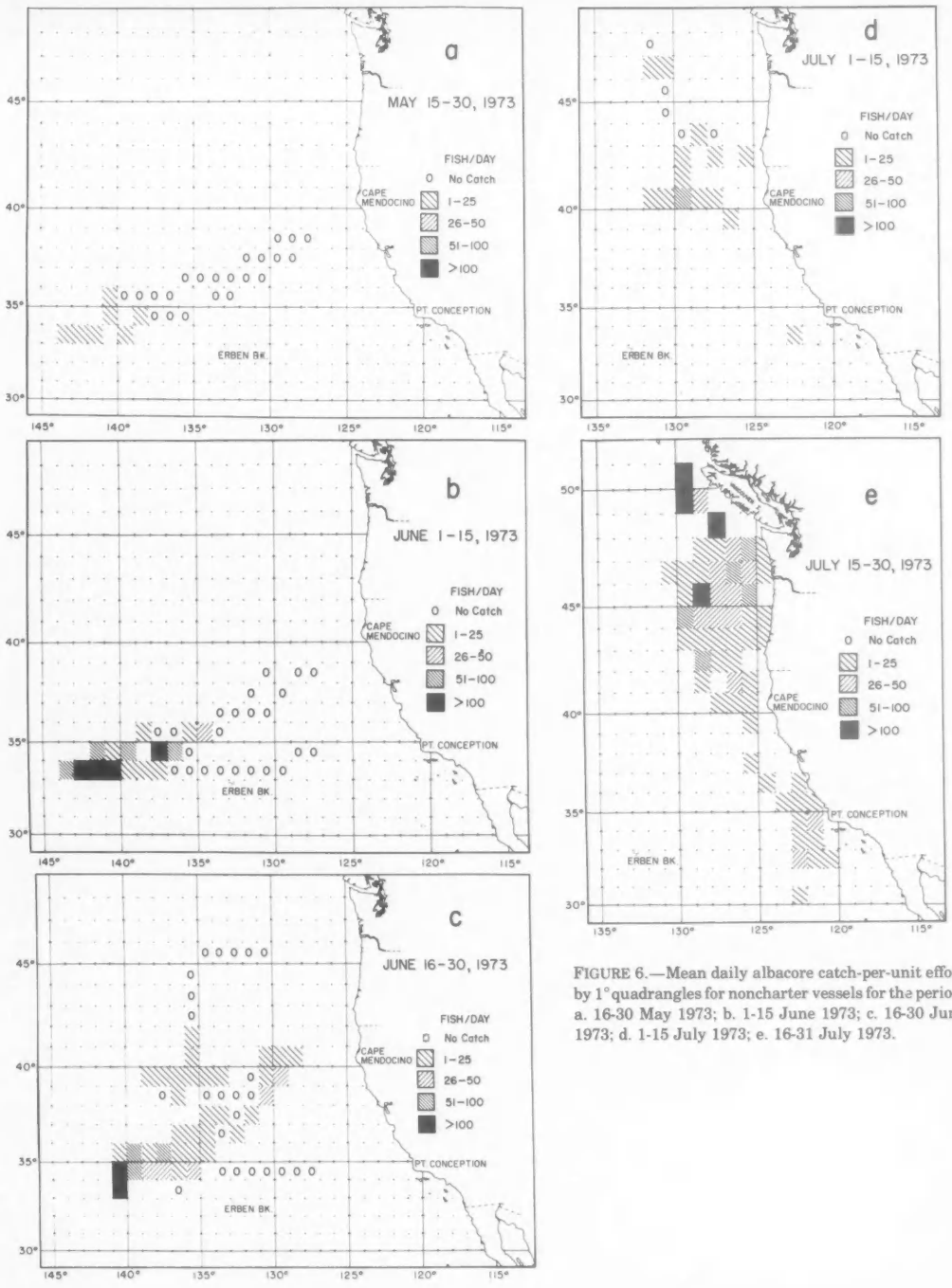


FIGURE 6.—Mean daily albacore catch-per-unit effort by 1° quadrangles for noncharter vessels for the period: a. 16-30 May 1973; b. 1-15 June 1973; c. 16-30 June 1973; d. 1-15 July 1973; e. 16-31 July 1973.

The last two charts in this series (Figure 6d, e, through the end of July 1973) reveal subsequent stages of albacore migration and commencement of the nearshore fishery. The relative abundance of albacore was high in nearshore waters by late July. In comparison to recent years, the 1973 nearshore fishery started about 3 weeks late.

SIZE COMPOSITION OF FISH

Three size modal groups of fish were caught in each year by the AFRF charter vessels; however, the relative proportions of the size groups varied among the years (Figure 7; Table 2). In 1972 about equal proportions of each size modal group were caught. In 1973 and 1974 the medium-size modal group was predominant and the larger one nearly absent.

TABLE 2.—Percentage size composition by number and by weight for albacore catches made by American Fishermen's Research Foundation charter vessels in the offshore area west of long. 130°W and south of lat. 38°N.

Year	<4 kg	4-8 kg	>8 kg	<4 kg	4-8 kg	>8 kg
	Percent by number			*Percent by weight*[1]		
1972	39	33	27	18	33	49
1973	43	53	4	25	65	10
1974	37	61	2	22	73	5

[1]Estimated from length-weight relationship given by Clemens (1961).

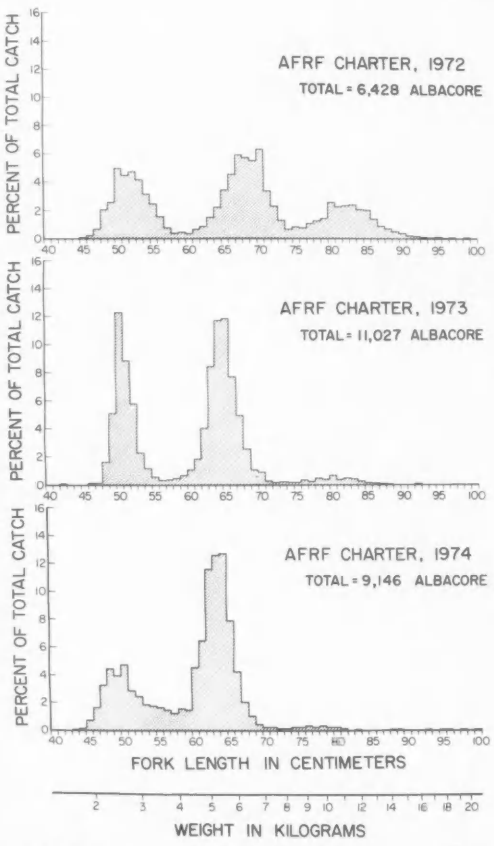


FIGURE 7.—Size composition by percent frequency of catch versus fork length for total catches of albacore from the research surveys in 1972-74.

THE MARINE ENVIRONMENT

Albacore were found mainly in Transition Zone waters. Variations in distribution and relative abundance between each of the surveys appeared to be related to oceanographic conditions of the Transition Zone. Transition Zone waters lie between the cool low salinity Pacific Subarctic waters to the north and the warm, saline Eastern North Pacific Central waters to the south and have temperatures and salinities that are characteristic of a mixture of these two primary water masses (Sverdrup et al. 1942; Christensen and Lee 1965). Transition Zone waters are found in a band across the North Pacific middle latitudes within the North Pacific Current and are bounded by sharp horizontal gradients in temperature and salinity (McGary and Stroup 1956; Roden 1970, 1972, 1975). These bounding gradient regions are sometimes referred to as the Subtropic and Subarctic fronts. The dynamic processes which produce and maintain these gradients also enrich these waters (McGary and Stroup 1956).

An oceanographic section of the vertical distribution of temperature and salinity was taken along long. 137°30'W in June 1972, 1973, and 1974 (Figure 8). In 1972 and 1973, Subarctic waters were found north of lat. 35 °N and Central waters south of lat. 31°30'N and 32°N, respectively. Boundaries of the Transition Zone between these water masses were well developed and readily identifiable. The Subarctic front was marked by abrupt shoaling of the 33.8‰ isohaline and 58°F (14.4°C) isotherm and a sharp horizontal gradient in salinity extending from the surface to greater than 175 m. The Subtropic front was delineated by steep shoaling of the 34.2‰ isohaline and 62°F (16.7°C) isotherm and a sharp gradient in salinity extending from the surface to greater

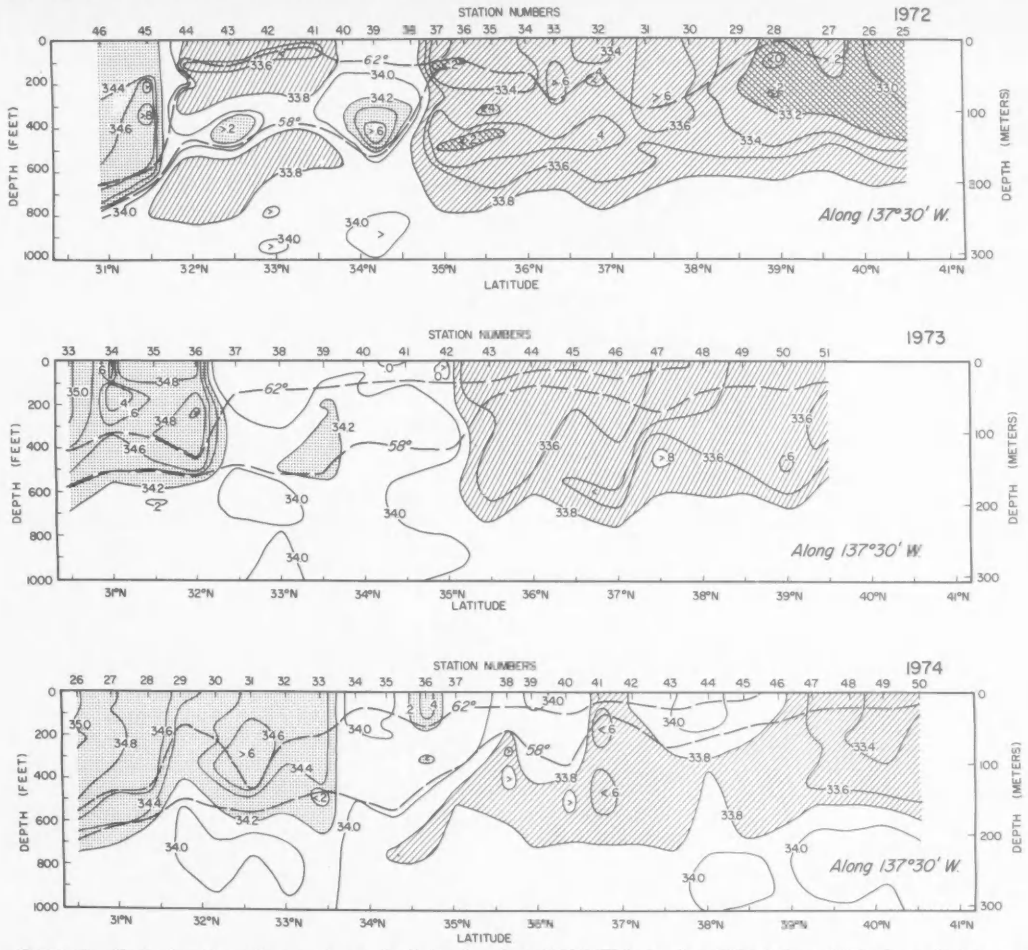


FIGURE 8.—Vertical sections of temperature and salinity along long. 137°30′W during June 1972, 1973, and 1974. Low salinity water (<33.8‰) indicative of Subarctic water is hatched and crosshatched. High salinity water (>34.2‰) indicative of Central water is shaded with a dot pattern. The 58° and 62°F isotherms are shown by heavy dashed lines.

than 150 m. A temperature gradient on the order of 0.6°C in 13 km was often found to mark these fronts at the sea surface. At other times, however, seasonal heating in the surface layer eroded the horizontal temperature gradient at the surface. Mixing was evident in the Transition Zone in 1972 with low-salinity water penetrating southward and some high-salinity water northward at intermediate depths.

Oceanographic conditions were different in the region of the Transition Zone in 1974 from those which were observed in 1972 and 1973. In 1974, boundaries of the Transition Zone were poorly developed and broken. Salinity gradients were diffuse and changes in depth of the isotherms gradual and variable in the regions of the Subarctic and Subtropic fronts. The Subarctic front was virtually nonexistent and Transition Zone waters graded gradually into Subarctic waters. The Subtropic front was weak and spread between lat. 31°30′ and 33°30′N. Saur[8] found that the diffuse

[8]Saur, J. F. T. 1976. Anomalies of surface salinity and temperature on the Honolulu-San Francisco route, June 1966-June 1975. NORPAX Highlights 4:2-4. (Unpubl. rep.)

nature of the Transition Zone and its frontal boundaries became evident late in 1973 and persisted throughout 1974.

ALBACORE CATCHES IN RELATION TO OCEANIC FRONTS

Graphical depictions of the frontal gradients that form the boundaries of the Transition Zone[9] and standardized albacore catches for June of each of the three surveys are shown in Figure 9a-c. This figure indicates that the catches were largely made within the Transition Zone in all 3 yr. During June 1972 and 1973, productive centers of fishing, indicating high relative abundance of albacore, developed in the Transition Zone between lat. 33° and 35°N and west of long. 135°W (Figure 9a, b). These centers persisted for several weeks before fishing effort was ended. In these years, the frontal structure was strongly developed and the Transition Zone easily identifiable. During June 1974 when the frontal structure was poorly developed and water mass boundaries were less distinct, catches were distributed over a larger range of latitude and longitude (Figure 9c). Overall catches in 1974 were substantial but they were not persistent in any area for more than a few days. Thus, while albacore were still associated with Transition Zone waters, the influence of extensive lateral mixing between water masses and the diffuse nature of the boundary frontal structure apparently failed to concentrate fish in a given location for periods of time as had apparently occurred in the previous 2 yr.

While graphical depictions of frontal structure outline the location of the boundaries associated with Transition Zone water (Figure 9a-c), they do not indicate the intensity of the gradients of the frontal structure. The frontal structure has been shown generally to have weak gradients during

[9]The temperature and salinity fields measured by the research vessel, augmented by the XBT data collected by the charter fishing vessels, were analyzed to delineate the frontal gradients.

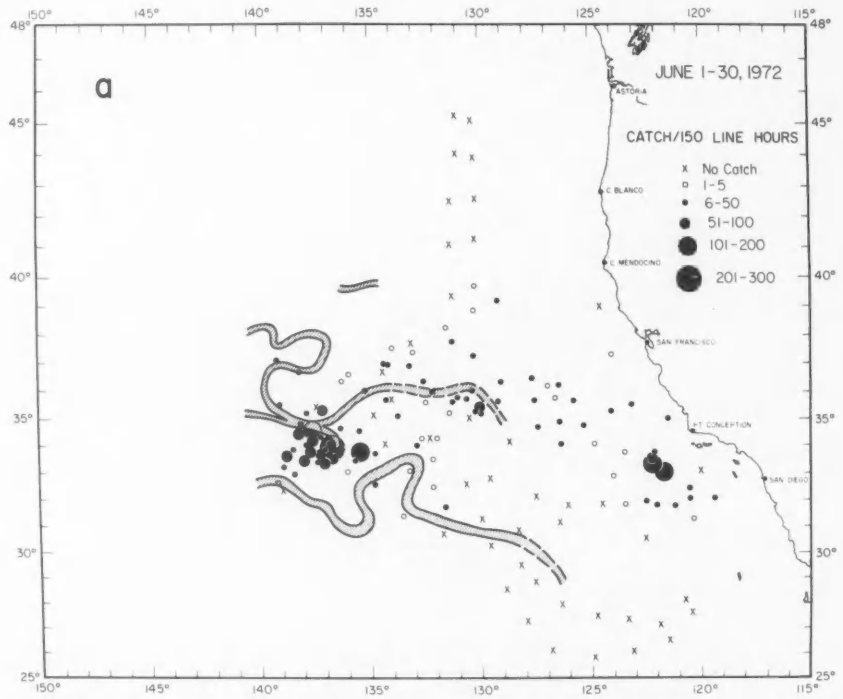
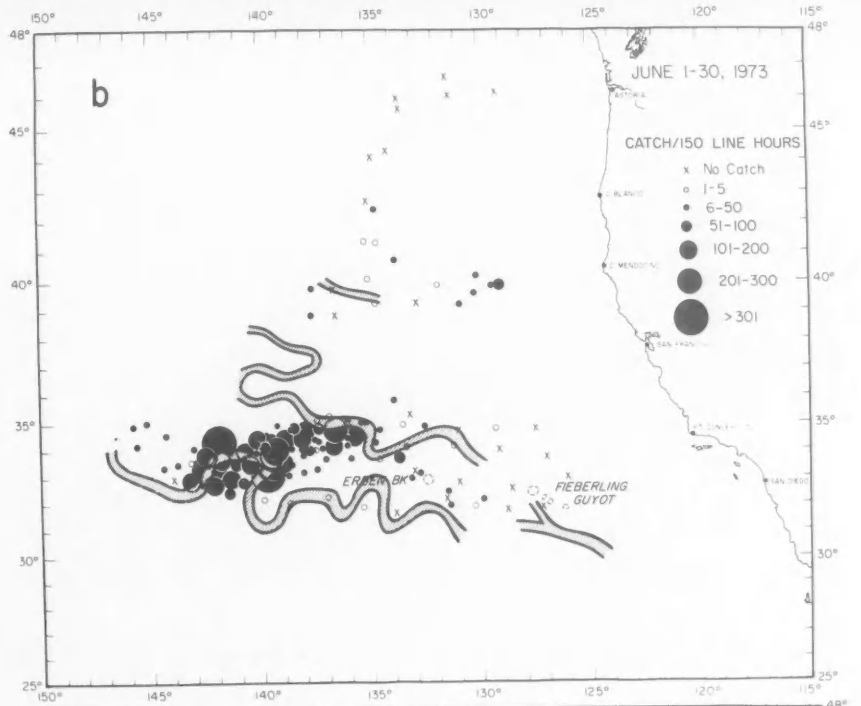
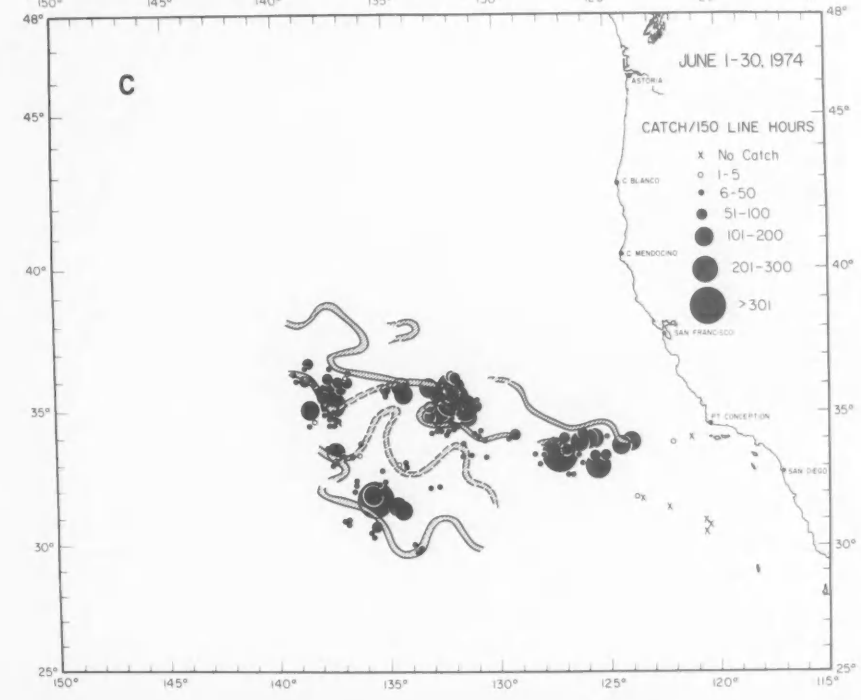


FIGURE 9.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels and locations of fronts delineating Transition Zone waters during: a. 1-30 June 1972; b. 1-30 June 1973; c. 1-30 June 1974.


b
JUNE 1-30, 1973
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ASTORIA
C. BLANCO
C. MENDOCINO
SAN FRANCISCO
PT. CONCEPTION
SAN DIEGO
ERBEN BK.
FIEBERLING GUYOT
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°


c
JUNE 1-30, 1974
CATCH/150 LINE HOURS
x No Catch
o 1-5
• 6-50
51-100
101-200
201-300
>301
ASTORIA
C. BLANCO
C. MENDOCINO
SAN FRANCISCO
PT. CONCEPTION
SAN DIEGO
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°

June 1974; however, one localized area did have sharp, abrupt gradients. The eastward protruding tongue of Transition Zone water centered at lat. 35°30'N, long. 132°30'W had salinity gradients comparable with those found in previous years. Substantial catches of albacore persisted in this one region for a week after which fishing effort was terminated.

Further information on the distribution of albacore can be derived from the catches made by the research vessels (Figure 10a-c).[10] The research vessels trolled for albacore along tracks that crossed the oceanic fronts and expended fishing effort in Central, Subarctic, and Transition Zone waters. With few exceptions, they did not catch albacore in Central or Subarctic waters. In 1972 and again in 1973, when a large meander developed in the Subarctic front, albacore were taken in the northward protrusion of Transition Zone water (Figure 10a, b). Albacore often were found close to the front. During each of the surveys, catches were made by the research vessel as the frontal gradients were being recorded by shipboard instrumentation.

Analyses of variance were performed upon the charter vessel catch data to test the hypothesis that catch rates were dependent upon water mass in the offshore area during June. For the 1972 survey, daily or twice daily XBT casts were matched with the daily catch data. Because specific isotherms were found to fall within very different depth ranges from one water mass to another, the dependence of catch rate upon classes of depth ranges for these isotherms was tested. Thus for this statistical test the water masses may be defined as follows:

Water mass	*Isotherm*	*Depth*
Pacific Subarctic	58°F (14.4°C)	<60 m
Transition Zone	58°F	≥60 m

[10]Catches are expressed in number of fish caught per 15 line-hours in 1972 and 1973 and per 60 line-hours in 1974. These numbers of line-hours approximate the amount of fishing effort expended each day by the research vessels during respective years.

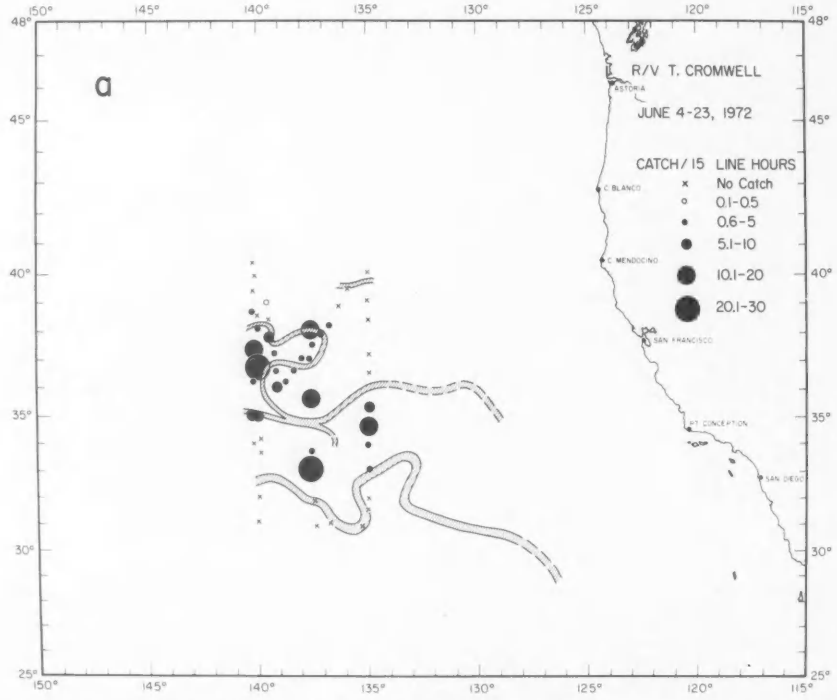
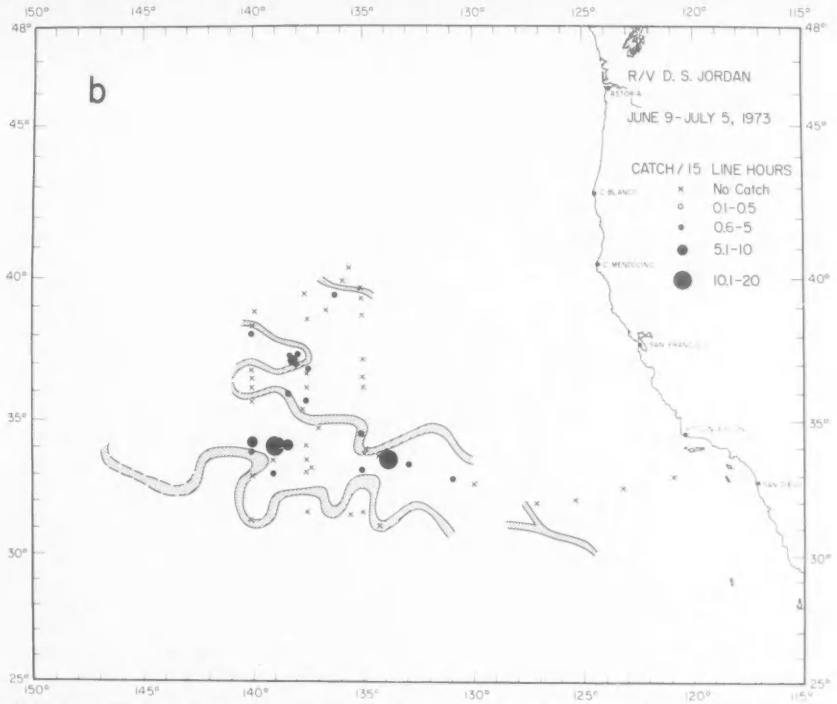
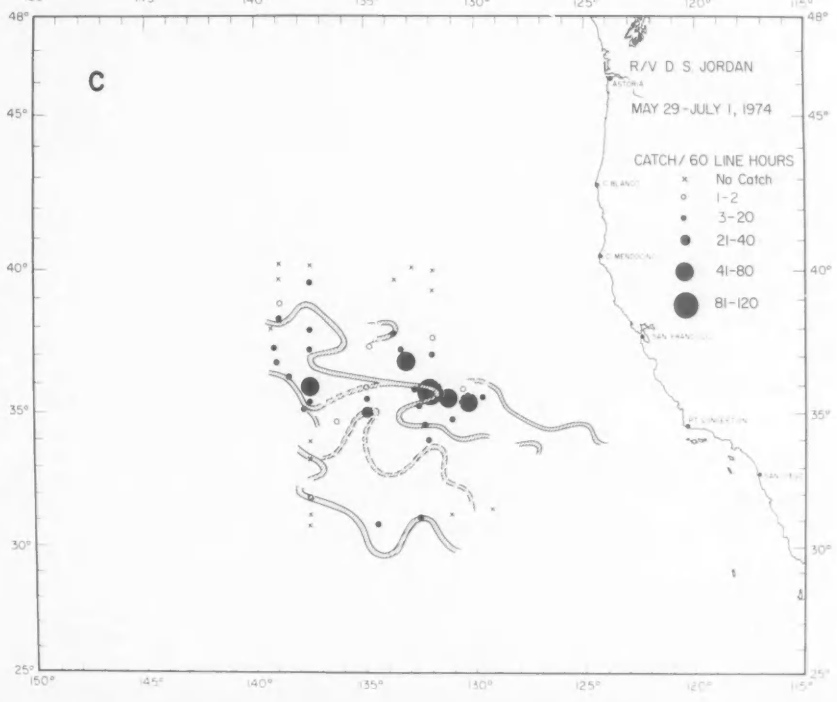


FIGURE 10.—Albacore catch per 15 line-hours by National Marine Fisheries Service research vessel and location of fronts delineating Transition Zone waters during: a. 4-23 June 1972; b. 9 June-5 July 1973; c. 29 May-1 July 1974.


b
R/V D. S. JORDAN
JUNE 9 - JULY 5, 1973
CATCH / 15 LINE HOURS
No Catch
0.1-0.5
0.6-5
5.1-10
10.1-20
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°


c
R/V D. S. JORDAN
MAY 29 - JULY 1, 1974
CATCH / 60 LINE HOURS
No Catch
1-2
3-20
21-40
41-80
81-120
150°
145°
140°
135°
130°
125°
120°
48°
45°
40°
35°
30°
25°

	62°F (16.7°C)	≤90 m
Pacific Central	62°F	>90 m

The data were transformed to logarithms in order to standardize between-sample variance. Results of the analysis of variance show that mean catch in the Transition Zone, which was greatest, is significantly different ($P = 0.01$) from those in other water masses.

For the 1973 survey, both charter and noncharter vessel catches were available for test. The fronts were assumed fixed for this time frame, as shown in Figure 9b, and catches were assigned to a water mass based upon reported geographic position. Because no fishing effort was expended in Central waters, except close to the Subtropic front where catches are expected, an analysis of this division could not be included. Both the charter and noncharter vessel data revealed that mean catches were significantly greater ($P = 0.01$) in the Transition Zone than those in the Subarctic waters.

The poor development of the boundary fronts between water masses during 1974 precludes a definitive assignment of catch to water mass; therefore, a test of the 1974 data was not considered.

Catches made by both the charter fishing vessels and the research vessel during each of the three surveys demonstrate that albacore are distributed within the Transition Zone and may be absent (or unavailable) or nearly so in water masses to the north and south during this phase of their shoreward migration. Relative abundance is high in offshore areas within the Transition Zone waters and at times close to the oceanic fronts that form the boundaries of Transition Zone waters. Further, when the oceanic fronts are diffuse and widely spread there is likely to be a corresponding spread in the distribution of albacore and a dislocation of the centers of high relative abundance.

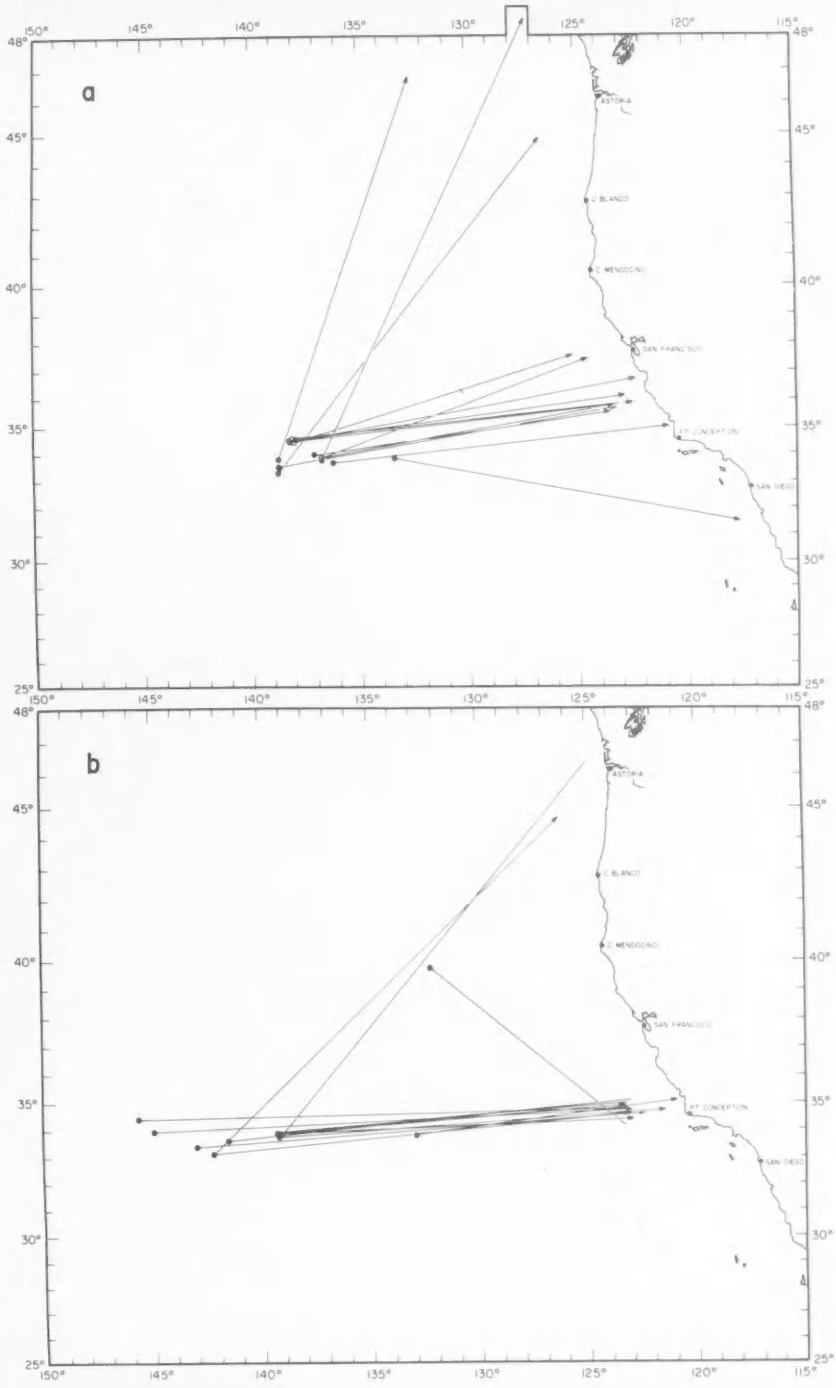
MIGRATION PATTERN FROM OFFSHORE TO NEARSHORE WATERS

We view the general pattern of seasonal migration of albacore into coastal waters where the U.S. fishery traditionally takes place during summer-fall as proceeding in three main stages: First, albacore migrate eastward from central North Pacific regions and form centers of high relative abundance within the eastern sector of the Transition Zone waters 600 to 1,000 mi off the coast. This development initially occurs in late May and June, a time when seasonal warming has raised the surface layer temperature of these waters to values considered to be within the habitat preference for albacore. These concentrations of fish may persist in offshore waters for several weeks. Next, as nearshore waters warm in ensuing weeks, albacore migrate toward coastal regions. Fishing efforts in the intervening zone usually produce only scattered catches, thus suggesting that during the shoreward migration the behavior of the fish is such that they are not available to fishing gear and/or that albacore may not be concentrated. Then, usually by mid-July, concentrations of high relative abundance are found near the coast, often in the vicinity of oceanic fronts related to coastal upwelling. Although variations may occur in this general pattern, the main features of the migration tend to repeat each year. The stages of shoreward migration and initial development of the albacore fishery can be seen in the two series of charts showing nominal catch per unit effort for 1973 (Figures 5a-e, 6a-e).

The shoreward migration of albacore from the central North Pacific into coastal waters appears to continue through the summer months. Albacore trolling experiments conducted from U.S. Navy picket vessels operating approximately between long. 130° and 135°W (Flittner 1963, 1964) showed albacore to be available there throughout the summer. Also, two albacore tagged by the Japanese in the western Pacific (near lat. 35°N and long. 171°E) in mid-June 1974 were recovered in the U.S. fishery in September 1974 (Japanese Fisheries Agency 1975).

Division in Migration Pattern

In order to examine migration of albacore from offshore to nearshore waters, an albacore tagging program was conducted during each of the offshore surveys. Over 4,500 albacore were tagged and released (Table 1). Recoveries of tagged fish made during the same season as released provide information on migration of albacore into nearshore waters (Figure 11a-c). Most recoveries of tagged fish made in 1972 of fish tagged during early season 1972 in waters offshore of long. 130°W were made in central-southern California waters and only a few recoveries were made in Pacific Northwest waters (Figure 11a). A similar recovery pattern was observed in 1973 (Figure 11b). A contrasting recovery pattern was observed in 1974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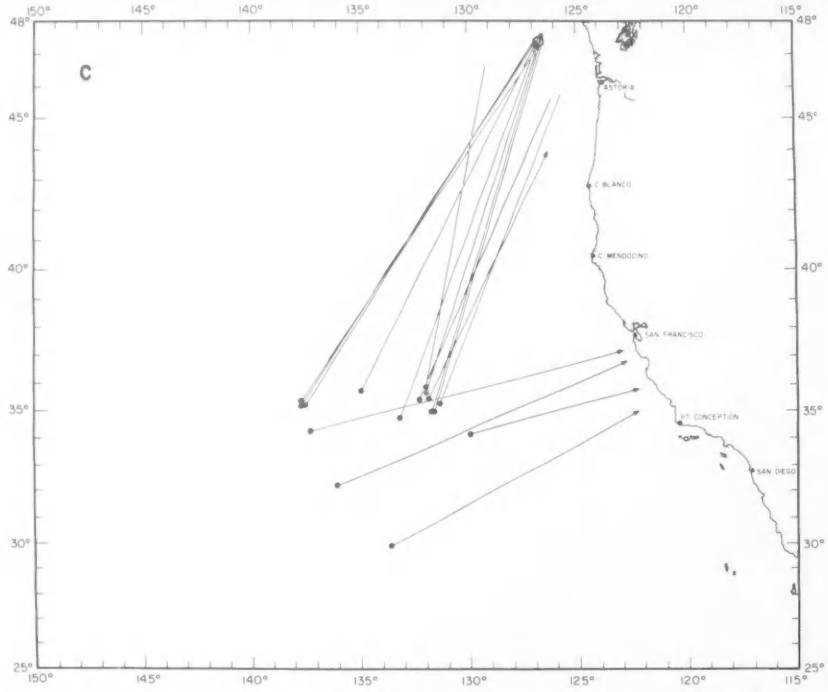

FIGURE 11.—Recoveries made during the same season as release of fish tagged during the early-season surveys in: a. 1972; b. 1973; and c. 1974.

when almost all of the recoveries of fish tagged in 1974 were made in waters off the Pacific Northwest (Figure 11c).

Differences in recovery pattern cannot be accounted for by geographic variations in fishing effort and fish catch. In all 3 yr, 70% or more of the fish caught during the commercial fishery was off the Pacific Northwest. It appears, instead, that differences in recovery patterns could be related to the location where tagged fish were released. In both 1972 and 1973, most of the tagging effort in offshore waters was between lat. 33° and 34°N and in 1974 it was farther north, between lat. 35° and 36°N. The different and divergent patterns apparently are the result of the albacore following different and divergent migration routes toward the nearshore waters. Tagging efforts of 1972 and 1973 and those of 1974 were apparently concentrated upon different branches of the migration. The division in the migration pattern appears to have occurred near lat. 35°N and must have occurred west of, and prior to, the appearance of the fish in the survey region.

Support for this proposed division in the migration pattern of albacore is indicated by differences in length-frequency distribution of albacore caught in the commercial fishery off California and north of California. Differences in size composition of fish caught in 1972 in the two regions (Figure 12 upper and lower) include: 1) the mode of large-size fish was about 5 cm larger in fish caught off California than in fish caught off the Pacific Northwest; 2) the mode of the medium-size fish, which formed the dominant size group in both regions, was 1 to 2 cm larger in fish caught off California than in fish caught off the Pacific Northwest; and 3) occurrence of three modal size groups taken in the fishery off California, but only two off the Pacific Northwest, where the smallest modal size group was absent. Examination of size-frequency distributions for 1973 and 1974 yielded similar results.

The size composition of albacore caught west of long. 130°W by charter vessels in 1972 (Figure 12 lower) was very similar to that for fish taken in the commercial fishery off California (Figure 12 mid-

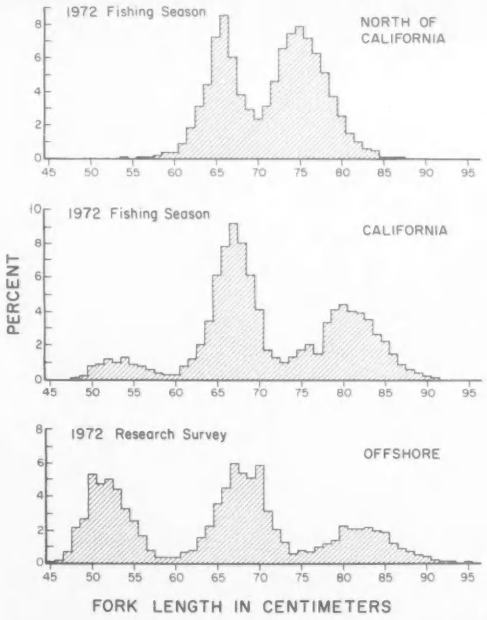

FIGURE 12.—Size composition of albacore caught by U.S. fishermen during 1972 north of California (upper), off California (middle), and size composition of albacore caught during the 1972 National Marine Fisheries Service-American Fishermen's Research Foundation offshore survey (lower).

dle) and hence different from the size composition of fish taken in the commercial fishery north of California (Figure 12 upper). It appears, then, that albacore caught in the offshore region of high relative abundance south of lat. 35°N in 1972 were a part of the migration of fish that reached regions off California.

We interpret the findings concerning offshore-nearshore and north-south geographic variations in size composition as supporting the hypotheses 1) that the fish which compose the fishery off California are separate from those which make up the fishery off the Pacific Northwest, and 2) that these two groups of fish follow different migration routes into nearshore waters.

Movements of Albacore by Size Groups

The size composition data for the 1972 charter vessel catch were stratified into offshore and nearshore regions at long. 130°W and into one 8-day and four 10-day time periods. Graphs of the stratified data standardized by fishing effort for 1972 (Figure 13) show that albacore initially appeared offshore near the end of May and there was an abrupt increase in relative abundance in the beginning of June. A decline in relative abundance was observed offshore after 19 June as centers of abundance shifted to nearshore where there was an increase in early July. Within these overall trends, changes in each of the three modal size groups can be followed. The mid-size modal group (fork length centered about 67 to 69 cm), initially dominated early offshore catches and then diminished in relative importance. It formed almost the entire catch of the first nearshore catches and continued to dominate nearshore catches into July. The large-size modal group (fork length centered about 82 to 85 cm) showed similar trends: a rise and fall in relative abundance offshore and with a subsequent shift to nearshore, but lagging behind the mid-size modal group by one 10-day period. The small-size modal group (fork length centered about 52 and 53 cm) was dominant offshore after 10 June but made little appearance in the nearshore region during the survey. This size group subsequently entered the nearshore fishery, however, as is evident from the size composition of the 1972 fishery off California (Figure 12 middle). An additional geographic division in

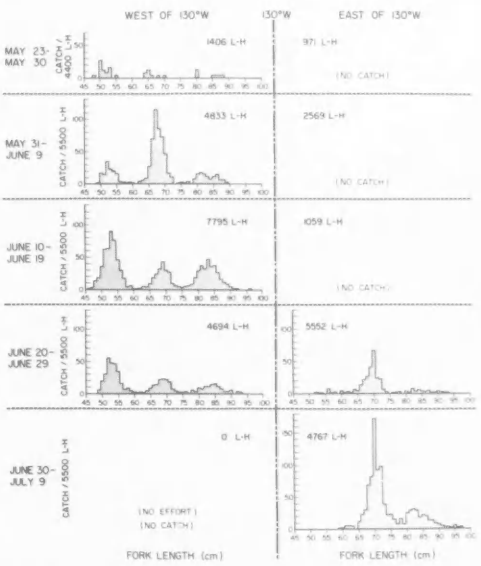

FIGURE 13.—Size composition of albacore caught by American Fishermen's Research Foundation charter vessels in 1972 by time periods and east and west of long. 130°W.

the offshore region, splitting the catch north and south of lat. 35°N showed that the catches first developed south of lat. 35°N and then moved north. By the fourth period (20 to 29 June), the small-size modal group composed almost the entire catch south of lat. 35°N and offshore of long. 135°W.

Several conclusions are evident from these temporal and areal changes in size composition. While catches persisted for up to 4 wk within a 2° by 4° quadrangle of latitude and longitude in the offshore region, changing patterns of size composition suggest that albacore were moving through the region within a period of 10 days or less and that the size groups migrated somewhat independently. The mid-size group, which composes the major portion of the U.S. fishery, led other size groups by 10 or more days. Also, the sequence of compositional changes of each size group and the geographic differences suggest that the migration from the offshore region to the nearshore fishery takes about 20 days or more; at least it did in 1972.

The 1972 catch data were chosen for examination of spatial and temporal changes in size composition because each of the size groups was well represented in the survey catches and all phases of the migration into the fishery are evident, including commencement of the fishery, by the completion of the survey. In 1973 the fishery started late, weeks after the survey, and in 1974 the patterns were less distinct, apparently in response to weak oceanic frontal conditions.

DISCUSSION

Association of Albacore Distribution With Oceanic Frontal Regions

The commercial fisheries on North Pacific albacore and the migration of albacore among these fisheries have frequently been associated with oceanic frontal regions in the western Pacific (Yamanaka et al. 1969; Uda 1973; other works), in the central North Pacific (Shomura and Otsu 1956; McGary et al. 1961), and in coastal upwelling regions (Pearcy and Mueller 1970; Panshin 1971; Laurs 1973; Laurs et al. 1977).

Results of our study provide evidence for the continuity of the association of albacore distribution with the Transition Zone and frontal boundaries into the eastern North Pacific. Catches made by the AFRF charter fishing vessels and the research vessel during each of the three surveys demonstrate that albacore are distributed mainly within the Transition Zone and usually are absent (or unavailable) in water masses to the north and south. Furthermore, our work strengthens the general concept that the distribution and relative abundance of large, highly migratory fish may be markedly influenced by oceanic frontal features. Other studies usually have had to rely on mean ocean conditions and/or statistically averaged fishery data, whereas our fishery and oceanographic data were collected concurrently during several surveys, and the amounts of fishing effort, fish catch, and oceanographic data were substantial.

Relative Abundance of Albacore in the Eastern Sector of the Transition Zone

We have found centers of high relative abundance of albacore in June within the eastern sector of the Transition Zone and often close to its frontal boundaries. Annual and intra-annual areal variations in relative abundance of albacore were observed and appeared to be related to development of the frontal boundaries of the Transition Zone. When the Subarctic and Subtropic fronts were strongly developed, areas of high relative abundance developed within relatively narrow bands in the Transition Zone and persisted for several weeks. When the Transition Zone was broader and the fronts were poorly developed, centers of high relative abundance were found over a larger area within the Transition Zone and did not persist for more than several days in any one location.

Based on scouting results from several research surveys, it appears that the timing and the location of fishing effort may be critical in locating centers of high relative abundance of fish in the eastern sector of the Transition Zone. In 1973, charter vessels first found a center of high relative abundance on 4 June near lat. 34°N, long. 140°W in Transition Zone waters. For several weeks prior to this finding, the AFRF charter vessels had made only scattered catches while scouting in and about this same area. Thus, it seems that the center of high relative abundance appeared in a surge within the first week of June. In 1955, an albacore survey cruise by a single U.S. Bureau of Commercial Fisheries (BCF) research vessel *(Hugh M. Smith)* scouted this area in late May and early June (Graham 1957). Seven longline sets and trolling conducted between lat. 41°and 28°N along long. 139°W resulted in only a single albacore

being taken before the vessel departed the area on 5 June. The 1955 scouting effort may have been too early by a matter of days to weeks to locate substantial numbers of fish. In 1957, a BCF fishery research vessel (*John R. Manning*) scouted to the north and east of this area in late June (Callaway and McGary 1959). Small to modest catches of albacore were made by trolling and in gill net sets in and about the Transition Zone, but the area which we have found to have a center of high relative abundance was not scouted.

Extension in Space and Time of U.S. Albacore Fishery

The cooperative NMFS-AFRF albacore research surveys have demonstrated the feasibility of extending the U.S. fishery for albacore in space and time. Albacore were caught by chartered fishing vessels in commercial concentrations considerably farther offshore than where the albacore fishery has traditionally taken place and up to 6 wk prior to the usual beginning of the fishing season. Noncharter commercial albacore fishing vessels, attracted to the early season offshore fishery by the research survey findings, have begun operating in this fishery in increasing numbers.

While fishing results of the AFRF-chartered and the nonchartered fishing vessels indicate that commercial amounts of fish can be caught earlier and farther offshore than the usual fishing season, additional experience is needed to examine the variability of this extension of the fishery, especially in terms of timing and availability, in order to judge properly whether it can provide a dependable contribution to the U.S. fishery. If in the long-run the early season offshore fishery proves viable, its development could be an important factor in reducing annual fluctuations in the catch of albacore. According to Clemens (1962) large annual fluctuations in catch are a prominent feature of the U.S. albacore fishery. Stabilization of catch among years could contribute significantly to the proper utilization and ultimately to the effective management of the resource.

The fishing success by charter and noncharter albacore commercial fishing vessels in 1972-74 is in contrast to an earlier attempt to establish commercial fishing in waters offshore from where the U.S. fishery has historically operated. According to McGary et al. (1961), an unsuccessful gill net and trolling effort was made in the summer of 1958 by a chartered commercial fishing vessel in areas of the central North Pacific where albacore were caught during research surveys conducted in summers of 1955 and 1956. The failure to catch albacore in amounts sufficient to support commercial fishing may have been an accidental event related to intense anomalous oceanic conditions which occurred ocean-wide and affected numerous fisheries in 1957-58 (Sette and Isaacs 1960).

Association of Shoreward Albacore Migration With Transition Zone and Possible Mechanisms

Shoreward Migration and Transition Zone

Based on association of albacore distribution and relative abundance with the Transition Zone and its frontal boundaries, we conclude that the shoreward migration of albacore is linked to the Transition Zone and that variations in the pattern of migration occur in response to variations in the character and development of the Transition Zone and its frontal structure. When the Transition Zone is narrow and its fronts are well developed, as in 1972 and 1973, the migration pattern of the fish is narrow and relatively well defined. In contrast, when the Transition Zone is broad and its fronts weakly formed, as in 1974, the migration pattern of fish is wide and less well defined.

There is also some suggestion that the strength and continuity of the Transition Zone fronts in offshore waters may affect the timing of arrival of fish in nearshore waters. When the fronts are well developed, fish appear to aggregate in their vicinity, resulting in a tendency for the fish to remain in offshore waters for periods of time that delay their arrival in the nearshore fishing grounds. However, when the fronts are weak the fish appear to move through offshore waters with less delay and arrive earlier in nearshore waters. Initial showing of fish in nearshore waters during the years of the surveys supports this speculation. The nearshore commercial fishery and sport fishery off southern California commenced several weeks later in 1972 and 1973 than in 1974.

Possible Mechanisms for Association of Albacore With the Transition Zone

The mechanisms responsible for the relationship between albacore and the Transition Zone and its frontal boundaries may result from a

number of factors acting in an interrelated matrix which impacts the fish both directly through physiological means and indirectly through forage availability. We postulate that the factors include, but are probably not limited to: 1) habitat temperature preference, 2) biological productivity, and 3) thermal gradients as they affect the albacore's thermoregulation processes, and that these factors act in an interrelated way superimposed on the innate drive of the fish to migrate across the North Pacific Ocean.

HABITAT TEMPERATURE PREFERENCE. — The distribution and relative abundance of albacore are related to sea-surface temperature (Clemens 1961; Johnson 1962; Panshin 1971; and others). The habitat temperature preference for albacore ranges from approximately 16° to 19°C (Clemens 1961; Laveastu and Hela 1970). This temperature range is found in the upper mixed layer waters of the Transition Zone in spring. Near-surface waters to the south of the Transition Zone are generally warmer than this and those to the north cooler.

The sequence of spring-summer warming of the surface layer along a section between Honolulu and San Francisco during 1972 is illustrated in Figure 14. The Transition Zone boundaries identified by the abrupt changes in depth of isotherms at intermediate depths fall between long. 130° and 140° W. The habitat temperature preference range for albacore (16° to 19°C) is shown with shading. In early and mid-spring (upper left) only the Central waters have preferred temperatures and these waters occur down to a considerable depth, almost 200 m. In subsequent time periods, a shallow sur-

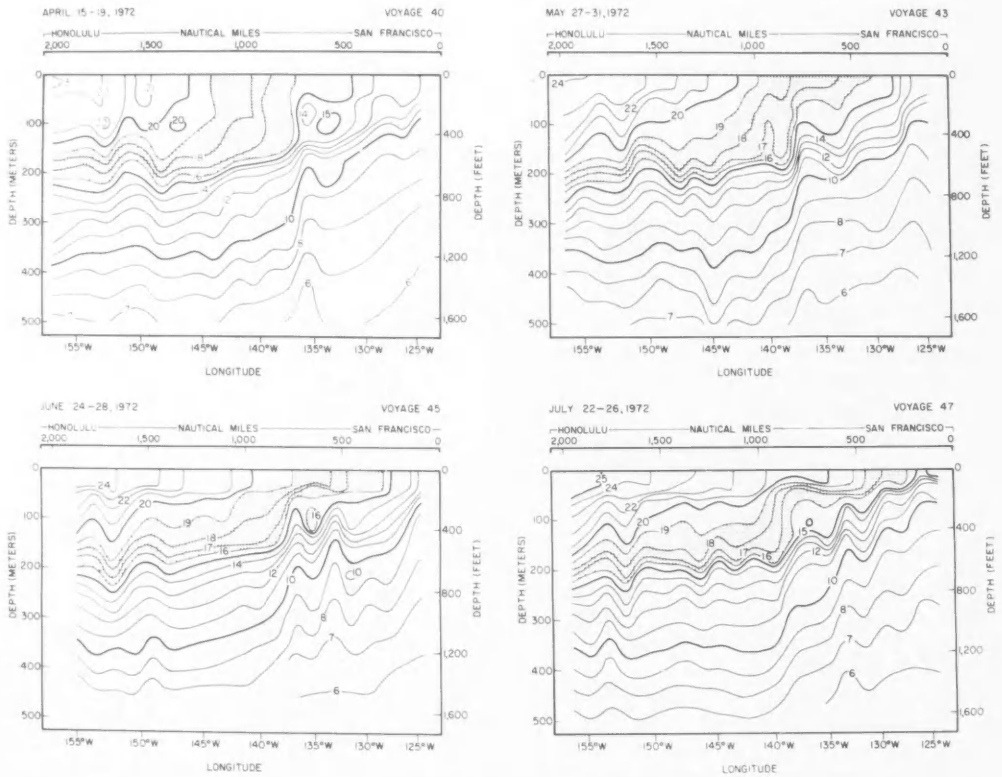

FIGURE 14.—Vertical temperature sections on a transect from Honolulu to San Francisco during April to July 1972. The temperature range between 16° and 19°C (60.8° and 66.2°F) is shaded.

face layer develops and warms to preferred temperatures, initially in the Transition Zone and then in more nearshore waters. It is near the end of May and through June that the preferred temperature range occurs in the Transition Zone and is generally restricted to depths <70 m. The depth limitation of preferred waters greatly improves the vulnerability of albacore to surface trolling gear.

BIOLOGICAL PRODUCTIVITY.—Tagging data show that migration of albacore from the western to the eastern North Pacific is active with an average migration speed of 48 km/day for 78- and 80-cm fish (Japanese Fisheries Agency 1975). This suggests that an albacore requires considerable energy to complete the transpacific migration. Sharp and Dotson (1977) calculated that the caloric expenditure per hour for a swimming albacore 63 cm in fork length is 5.02 kcal/h. They also speculated that fat stores may be an important energy source utilized by albacore for migration. Studies of the food habits of albacore caught during the surveys[11] show that albacore feed actively in offshore waters during their shoreward migration. The composition of the food found in the stomachs is different from that of fish caught in inshore waters (Pinkas et al. 1971, Laurs and Nishimoto MS[12]), but average volumes of food in stomachs from the two regions are similar. Therefore, availability of forage is likely to be an important factor influencing the route of albacore migration.

There are three major oceanic habitats in the North Pacific which are separated by pronounced latitudinal faunal boundaries and steep latitudinal gradients in standing stocks of phytoplankton and zooplankton (McGowan and Williams 1973). These species and biomass boundaries are coincident with the boundaries of the Pacific Subarctic, Transition Zone, and Pacific Central waters (Johnson and Brinton 1963). A northward increasing step-cline occurs among the North Pacific habitats in standing stocks of phytoplankton (Venrick et al. 1973; McGowan and Williams 1973), zooplankton (Reid 1962; McGowan and Williams 1973), and micronekton (Aron 1962), and in primary production (Koblents-Mishke 1965). Zooplankton and micronekton standing stock estimates made during the offshore albacore surveys show similar results with values generally being highest in Subarctic waters, intermediate in Transition Zone waters, and lowest in Central waters.

Since biological productivity is higher in Subarctic waters than in Transition Zone or Central waters, it would be most advantageous from the standpoint of food availability for albacore to confine their migration path to Subarctic waters. However, during spring months the temperature of the Subarctic waters is much lower than the habitat preference for albacore. We conclude, then, that the northern limit of the albacore migration route during spring is determined by ocean temperature and that the limiting temperature is found near the northern boundary of the Transition Zone. The temperature of the upper layer of the Central waters is higher than the habitat temperature preference for albacore, but there are temperatures below the upper layer which lie within the habitat temperature preference for albacore. Thus, temperature could restrict the distribution of albacore from the upper layer but not at some depth interval below the upper layer. We propose that while temperature may play a role in determining the southern limit of the albacore distribution and migration route, the major factor is the abundance and availability of forage organisms which drop off sharply near the southern boundary of the Transition Zone.

OCEAN THERMAL GRADIENTS AND THERMOREGULATION OF ALBACORE.—Thermoregulation processes by albacore may be an important factor in determining their association with the Transition Zone and its frontal boundaries. Thermoregulation is characteristic of tunas and certain other fishes (Carey et al. 1971). According to Neill (1976) for fishes as a group, the only effective means of regulating body temperature is by behavioral regulation of the immediate environmental temperature through locomotory movements.

Computer simulation models developed by Neill (1976) indicate that where environmental conditions are characterized by large expanses of isothermal or nearly isothermal water separated by relatively narrow thermal discontinuities (e.g., oceanic frontal systems), fishes will be relatively concentrated near the discontinuities.

[11]Laurs, R. M., and R. N. Nishimoto. 1973. Food habits of albacore caught in offshore area. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1973, p. 36-40. (Unpubl. rep.)

[12]Laurs, R. M., and R. N. Nishimoto. Food habits of albacore in the eastern North Pacific. (Unpubl. manuscr.)

Division in the Migration of Albacore Into the American Fishery

Our study indicates that there is a division in the migration pattern of albacore into the American fishery with fish which compose the fishery off the Pacific Northwest and off California following different routes. We believe that the "northern" branch of the migration progresses as described by Powell et al. (1952) who, during an exploratory albacore fishing survey over a region off the Pacific Northwest, found albacore along a warm-water edge that develops seasonally 400 to 500 n.mi. offshore of southern Oregon in late June and early July. The warmwater edge was observed to progress northward and coastward in a bulge or pouchlike pattern as seasonal warming of the surface waters took place over the ensuing weeks. The occurrence of albacore was found to follow the progression of the warmwater zone shoreward and northward along the coasts of Oregon and Washington and by mid-August to waters off the Queen Charlotte Islands, British Columbia. Powell et al. (1952) concluded that these findings, as well as earlier observations, indicated that the main barrier directly or indirectly influencing the distribution of albacore throughout their northern range is water temperature.

Clemens (1961) investigated the onset and movements of the albacore fishery off California and Baja California for the fishing seasons 1951 through 1953. From catch records he found that albacore entered the coastal waters as far south as 200 n.mi. south of Guadalupe Island (lat. 29°N) in some years and as far north as the San Juan Seamount (lat. 33°N) in others. He also presented tag recovery data which showed that albacore move from Baja California or southern California in the early season northward to central California as the season progresses (however, only one recovery of a tagged fish was made off northern California). Clemens concluded that albacore entering the American fishery initially migrate to Baja California or southern California and that longshore movement was the dominant mode of their dispersal into coastal zones to the north. Although he allowed that albacore may reach Oregon and Washington waters by following the seasonal bulge of warm offshore water as suggested by Powell et al. (1952), Clemens stated that a large part of the main body of albacore travel northward up the coast to waters off the Pacific Northwest from Baja California and southern California. No evidence was given for this statement and our newer findings do not support it. We concur that northward longshore movement is important in nearshore waters, but conclude that fish entering waters off Baja California or southern California do not migrate farther north than about San Francisco before leaving the American fishery.

Flittner (1963) presented a schematic diagram of albacore movement off the Pacific coast based on albacore catches made by U.S. Navy picket vessels during 1960-62. The picket vessels, stationed 200 to 500 n.mi. offshore (no farther west than long. 135°W) and spaced at latitudinal intervals of 300 n.mi., each trolled several jig lines from May through October. Flittner said that albacore appeared to congregate within an "optimum-temperature" zone and seem to split into two migratory components. Early arrivals proceed to southern feeding areas and late arrivals turn to the northern area, each movement depending upon the progression of seasonal warming.

Progression of seasonal warming continues to appear to be an important factor affecting paths of albacore migration. However, influence of the Transition Zone development and the division of migration pattern described here add considerable complexity to earlier ideas. Our findings suggest that events in offshore waters are important in determining the distribution and relative abundance of albacore in coastal waters.

Pacific Northwest and California Groups of Fish

Based on offshore-nearshore and north-south geographic variations in size composition of albacore we postulate that the group of fish which compose the albacore fishery off California are separate from those which make up the fishery off the Pacific Northwest. Brock (1943) arrived at a similar conclusion after comparing length-frequency distributions of albacore landed in San Pedro, Calif., and Astoria, Oreg. Brock found differences in size composition and stated, "This would argue that the schools of fish off the Oregon coast were not a part of the schools appearing off the California coast, even though, as indicated above, the two groups may have had a common origin... The time of arrival of fish and their abundance as shown by the monthly commercial catch for the ports discussed here (San Pedro and Astoria) make it seem likely that at least two separate groups of schools invaded the coastal

area, one in the north off Oregon and the other in the south off southern California."

Results of studies on the artificial radionuclide ^{60}Co in albacore provide additional evidence that the "northern" and "southern" groups of fish are independent. Krygier and Pearcy (1977) found that the peak activity levels of ^{60}Co in albacore off Oregon occurred a year earlier than the peak activity levels seen by Hodge et al. (1973) off southern California. According to Krygier and Pearcy, the heaviest fallout input of ^{60}Co into the North Pacific occurred at about lat. 40°N. They speculated that due to circulation in the North Pacific, albacore which were associated with waters north of lat. 35°N could have experienced high levels of ^{60}Co up to a year before the tuna associated with waters to the south. They concluded that, "Circulation in the North Pacific and the latitudinal differences in the location of the two portions of the albacore population [as proposed by Laurs and Lynn in this paper] appear to be a plausible explanation for the difference of 1 yr in activity peaks between albacore caught off Oregon by us and those off southern and Baja California by Hodge et al. (1973)." Thus, strong evidence from several independent sources points toward two separate groups of albacore following separate migration paths.

ACKNOWLEDGMENTS

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BIOLOGY OF THE SUMMER FLOUNDER, *PARALICHTHYS DENTATUS*, IN DELAWARE BAY[1]

RONAL W. SMITH AND FRANKLIN C. DAIBER[2]

ABSTRACT

Data on the age, growth, food habits, and racial characters of summer flounder, *Paralichthys dentatus*, from Delaware Bay were examined. Fish were present year-round, although 95% were taken from May through September, and no mature fish were caught during the winter. Fish were aged from annuli on the largest left otolith. The growth rate for males was described by $L_{t+1} = 141.91 + 0.767(L_t)$, and for females $L_{t+1} = 136.72 + 0.843(L_t)$. The Delaware Bay commercial fishery in 1966 was primarily supported by age-groups 2 through 5. The total length-weight relationship was described by, log weight (grams) = log 0.404×10^{-5} + 3.151 log [total length (millimeters)], and the total length-standard length relationship by, total length (millimeters) = 16.695 + 1.55[standard length (millimeters)]. Age and sex made no significant difference in meristic character evaluation. The reported range of variation for some characters was extended: dorsal rays, 89-98; anal rays, 63-78; pectoral rays, 10-13; vertebrae, 40-43; standard length/head length, 3.64-4.30; and head length/upper jaw length, 1.54-2.26.

One objective of this study was to investigate the age, growth, and food habits of summer flounder, *Paralichthys dentatus* (Linnaeus), caught in Delaware Bay. Previous research on age and growth, Eldridge (1962) and Poole (1961), disagreed and additional study was needed.

A second objective was to determine the magnitude of variation in meristic characters of summer flounder from Delaware Bay for comparison with other geographic areas. Ginsburg (1952) reported that summer flounder from Chesapeake Bay and from Beaufort, N.C., might belong to two distinct racial stocks on the basis of gill raker frequency distributions. According to Poole (1966), unpublished studies found no real differences between these populations, but he added that analysis of racial data from Maryland, Virginia, and North Carolina areas suggested the need for additional research.

Summer flounder are common from Cape Cod to North Carolina and they have been reported from Maine to Texas (Bigelow and Schroeder 1953; Poole 1962). They normally inhabit coastal and estuarine waters during the warmer months of the year and move off on the continental shelf in 20 to 100 fm of water during the fall and winter (Bigelow and Schroeder 1953). Spawning occurs during the fall and winter while the fish are moving offshore or at their wintering location, and larvae and postlarvae drift and migrate inshore to coastal and estuarine nursery areas (Smith 1973).

COLLECTION OF MATERIAL

Most fish examined were caught by a 9-m (30-ft) otter trawl, 7.6-cm (3-in) stretch mesh in the body and 5.1 cm (2 in) in the cod end, during monthly fish survey trips in Delaware Bay. A total of 13 sectors were sampled during the period August 1966 through November 1971 (Figure 1), with a minimum of 3 and a maximum of 12 sampled in any 1-mo interval. Sectors sampled were selected to cover a range of salinities and depths in Delaware Bay. During the summer of 1968, three sectors were sampled during the day and again that night. Sampling at each station consisted of making a Nansen cast within 2 m of the bottom for temperature and a water sample, and trawling for 30 min. The mean tow length was 1.2 n.mi. Average water depth for each tow was determined by eye from a recording fathometer trace. Some fish were taken by beach seining, while others were caught during miscellaneous trawling operations through February 1973.

Stomachs for gut analysis were removed immediately on fish capture and placed in 95% isopropyl alcohol.

The commercial summer flounder catch from

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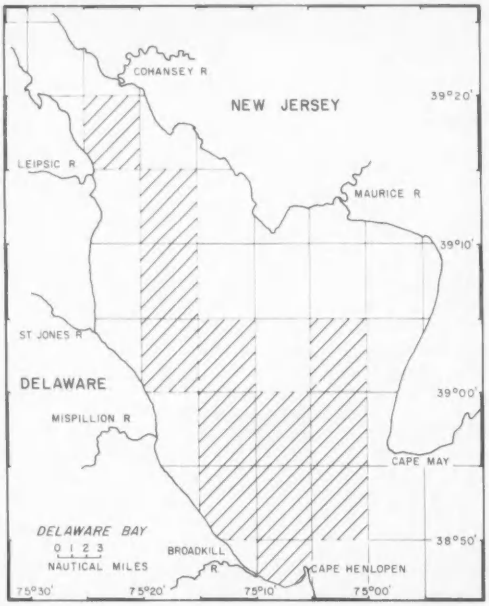

FIGURE 1.—Delaware Bay with sampling sectors shaded.

Delaware Bay was sampled on four occasions in 1966 by measuring all (1,060) fish caught by a 14-m trawler using both a 15-m (50-ft) otter trawl, body—7.6-cm (3-in) stretch mesh, cod end—5.1 cm (2 in), and a 16-m (52-ft) otter trawl, body—10.2 cm (4 in), cod end—7.6 cm (3 in). This vessel was typical of the few commercial boats operating in the bay then, and 1966 was the last year trawling was permitted.

GENERAL OBSERVATIONS

Summer flounder seem to have a ubiquitous range in Delaware Bay. They were caught in all sectors sampled; and in water with temperatures from 1.6° to 26.8°C, salinities from 10.6 to 31.8‰, and depths from the shore to 25 m. Most (95%) fish were caught from May through September. A few juvenile fish were taken in every winter month, indicating that some juveniles move to deeper parts of the estuary during the winter rather than offshore. Poole (1966) suggested a similar phenomenon for estuaries in North Carolina.

During the 5-yr survey, the yearly mean number of summer flounder caught per nautical mile of trawling (number of fish caught per year divided by the total length of tows containing summer flounder) varied from 1.5 to 4.7, with no significant trend. No real difference was apparent in the number (34 day versus 29 night) of flounder caught between day and night tows.

AGE AND GROWTH ANALYSIS

Otoliths were used for aging fish because they were much easier to read than scales, and both Poole (1961) and Eldridge (1962) found them suitable for aging. Left and right otoliths were examined, and we found the radial length (distance from the center of the core to the anterior tip) was different between left and right ones from the same fish. This occurred because the center area or core (Figure 2) was located more posteriorly in the right otolith. We did not compare left and right otoliths to see if the relationship between radial length and the various annuli lengths were the same for both.

Left otoliths were removed from all flounder (either fresh or previously frozen) caught in

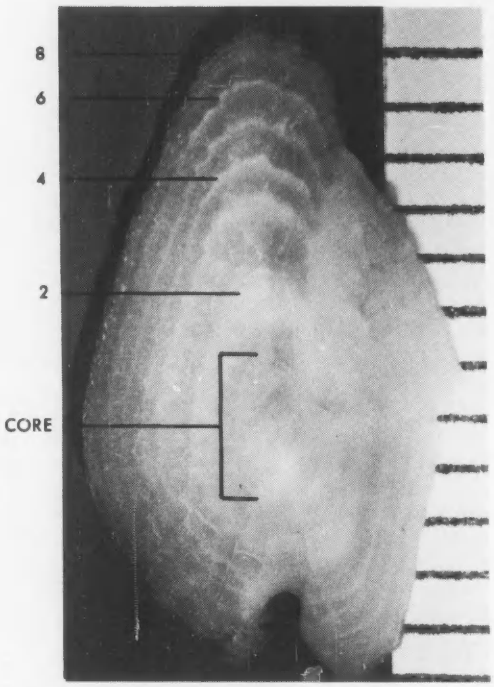

FIGURE 2.—Left otolith from an age-group 8 summer flounder, total length 69 cm, with estimated age indicated against respective annuli (rule marking in millimeters).

1966-68. Upon removal, they were cleaned in water and stored dry. Prior to examination, otoliths were soaked for 30 min in a 2% solution of the plant enzyme, papain, according to the technique of Pruter and Alverson (1962) for cleaning and clearing. Annuli were visible before soaking and it is doubtful this clearing process helped.

For examination, otoliths were placed in distilled water in the wells of a Coor's[3] black porcelain spot plate. They were measured with an ocular micrometer to the nearest 0.1 mm for radial length and annuli lengths with the concave surface up. All otoliths were read twice, and those very difficult to interpret a third time. Approximately 20% of the otoliths were discarded because of irregular shape or indistinct annuli, leaving 319 used in the age analysis. Mean annuli lengths are given in Table 1. No age-group 6 males were collected in this study.

There was a linear relationship between total length (TL in millimeters) and otolith radial length in millimeters, and this relationship was best described by:

$$\text{Otolith radial length} = 0.012(\text{TL})$$

$$\text{Correlation coefficient} = 0.998$$
$$\text{Standard error of estimate} = 0.336$$

This equation applied to both sexes.

Fish length at time of annulus formation or back-calculated length was calculated as described in Rounsefell and Everhart (1953), and these lengths for males and females are given in Tables 2 and 3, respectively. No correction factor was used in the calculation because: 1) the line best representing the total length-otolith radial length relationship had a zero origin and 2) correction factors obtained were not reasonable because they gave the fish a negative length at time of otolith formation. According to Rugh (1962), who used *Fundulus heteroclitus* as an example of a typical teleost, otoliths start to form in the first quarter of development. Therefore, fish length at time of otolith first formation could be considered negligible when compared with fish length at 1 yr.

The observed 17 cm length at 1 yr as reported by Eldridge (1962) is far above a 12 cm length we back-calculated using the otolith core edge as the first annulus. We assumed the first annulus was located at the core edge (radial length from 1.1 to 1.5 mm) because typically the first well-defined annulus away from the core (approximately 3.3 mm radial length, Table 1) was only present in otoliths from fish larger than 27 cm, fish we believed too large to be in age-group 1 (fish 1 or 1+ yr old). Supporting our belief is Eldridge's reported length frequency at 1 yr and our subsequent capture (1973) of Delaware Bay flounder during winter in the 15-20 cm size range. A few otoliths we examined had faint rings at radial lengths of 2.0 to 2.6 mm, but we thought these represented a false annulus. Probably these faint rings were true first annuli and they were not observed in most otoliths.

The primary reason for the difference between our back-calculated fish lengths and those given by Poole (1961) and Eldridge (1962), Tables 2 and 3, is the interpretation of age at the first annulus used. Examination of Poole's calculated length at 1 yr plus his photographs of otoliths indicated he considered the first well-defined annulus as being

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Mean radial distance ± 1 standard deviation of annuli on otoliths from summer flounder taken in Delaware Bay during 1966-68. (No suitable first annulus was found.)

Age-group	Number of otoliths	Measured radial distance for successive annuli (mm)						
		2	3	4	5	6	7	8
Male:								
2	44	3.3±0.3						
3	51	3.2±0.3	4.2±0.3					
4	23	3.2±0.3	4.2±0.3	4.9±0.2				
5	11	3.2±0.2	4.2±0.2	4.9±0.3	5.4±0.3			
7	1	3.0	4.3	4.8	5.6	6.1	6.4	
Female:								
2	50	3.4±0.2						
3	71	3.4±0.2	4.6±0.3					
4	36	3.3±0.3	4.6±0.3	5.5±0.3				
5	22	3.3±0.3	4.6±0.4	5.4±0.4	6.0±0.4			
6	4	3.4±0.1	4.7±0.2	5.6±0.3	6.4±0.4	7.1±0.4		
7	3	3.2±0.1	4.3±0.6	5.3±0.5	6.2±0.4	7.1±0.7	7.9±0.8	
8	3	3.2±0.3	4.3±0.5	5.1±0.4	5.7±0.5	6.3±0.6	6.8±0.6	7.2±0.6

TABLE 2.—Mean back-calculated total length ± 1 standard deviation and annual percent increase in mean total length for male summer flounder captured in Delaware Bay during 1966-68. Included for comparison are mean back-calculated lengths from other studies.

Age-group	Number of fish	Back-calculated length at successive annuli (mm)							
		1	2	3	4	5	6	7	8
2	44		277 ±20						
3	51		261 ±23	344 ±16					
4	23		258 ±21	342 ±17	400 ±14				
5	11		261 ±12	348 ±10	403 ± 9	445 ±11			
7	1		242	347	388	452	493	517	
Mean length			260	345	397	448	493	517	
Annual % increase			24.6	13.1	11.4	9.1	4.6		
Poole (1961)	251	326		387	427				
Eldridge (1962)[1]	170	240		319	357	381	399	414	426

[1]Lengths given for Eldridge at the end of year 1 and 2 are estimates of the average observed length frequency.

TABLE 3.—Mean back-calculated total length ± 1 standard deviation and annual percent increase in mean total length for female summer flounder captured in Delaware Bay during 1966-68. Included for comparison are mean back-calculated lengths from other studies.

Age-group	Number of fish	Back-calculated length at successive annuli (mm)								
		1	2	3	4	5	6	7	8	9
2	50		301 ±21							
3	71		280 ±19	383 ±21						
4	36		279 ±25	389 ±24	465 ±25					
5	22		289 ±20	399 ±24	470 ±22	526 ±22				
6	4		273 ±23	379 ±33	450 ±21	512 ±22	568 ±25			
7	3		252 ±12	332 ±48	412 ±34	484 ± 5	553 ±16	612 ±19		
8	3		289 ±12	395 ±20	469 ± 6	521 ±12	575 ±18	624 ±14	661 ± 9	
Mean length			280	380	453	511	565	618	661	
Annual % increase			26.3	16.1	11.4	9.6	8.6	6.5		
Poole (1961)		271	377	465	531	644				
Eldridge (1962)[1]		170	240	377	424	471	518	566	613	657

[1]Lengths given for Eldridge at the end of year 1 and 2 are estimates of the average observed length frequency.

formed at the end of the first year. Eldridge decided that Poole's calculated length at 1 yr seemed too high when compared with observed length frequencies, so he considered this first well-defined annulus to be formed at first spawning, or at the end of the flounder's third year. We considered the first well-defined annulus to be formed at age 2. Therefore, Poole's age 1 fish = our age 2 fish = Eldridge's age 3 fish. Work by Richards (1970) supported our age interpretation. He found summer flounder growth curves generated by analog simulation only fit Poole's length data when Poole's age-groups were shifted 1 yr forward, i.e., his age 1 fish were made age 2. Richards did not examine Eldridge's age data.

Comparing Poole's (1961) lengths to ours after adjustment for age interpretation, we find them similar except for age 5 females. With age interpretation adjustment, Eldridge's (1962) lengths for males are smaller than ours except at ages 2 and 3 when they are larger, and his lengths for females are noticeable larger until age 5 when they begin to agree quite well.

The length-frequency distribution of the 1966 commercial catch and the 1966-71 research catch revealed that both were primarily composed of age-groups 2 through 5. Figure 3, using the 1966 and 1968 research catch because lengths were by sex, is representative of this distribution. This age composition is similar to the age composition reported by Poole (1961) for the sport fishery catch of Great South Bay, N.Y., after adjustment is made for age interpretation differences.

Equations representing growth rates from Walford's growth transformation (Rounsefell and Everhart 1953) are:

$$\text{for males} \quad L_{t+1} = 141.91 + 0.767\,(L_t)$$

$$\text{Correlation coefficient} = 0.996$$
$$\text{Standard error of estimate} = 7.39$$

$$\text{for females} \quad L_{t+1} = 136.72 + 0.843(L_t)$$

$$\text{Correlation coefficient} = 0.998$$
$$\text{Standard error of estimate} = 6.20$$

where L_{t+1} = fish length (millimeters) at time t plus 1 yr

L_t = fish length (millimeters) at time t.

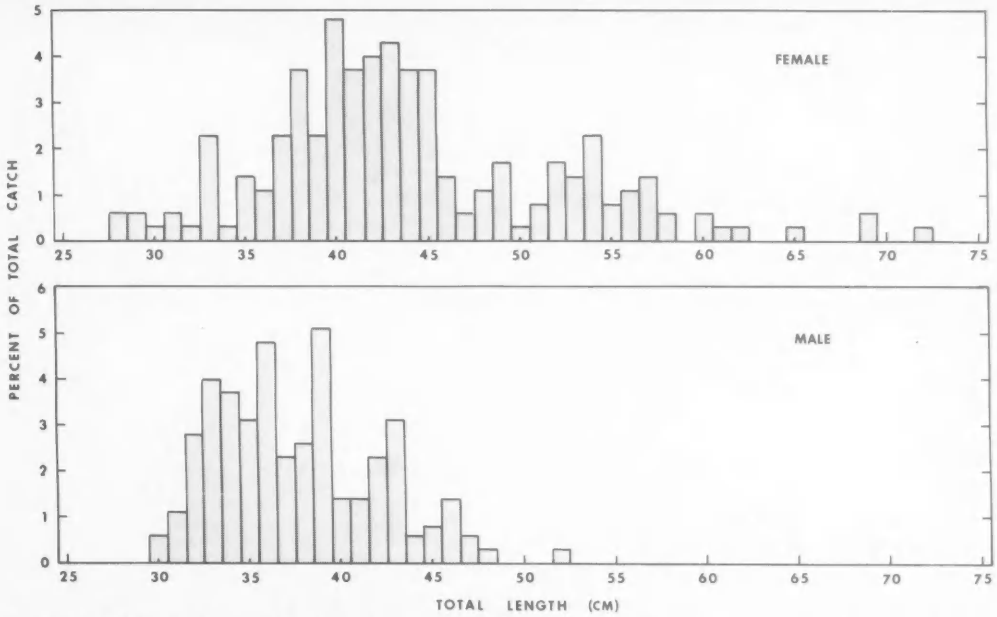

FIGURE 3.—Total length-frequency distribution for 149 male and 202 female summer flounder caught in Delaware Bay in 1966 and 1968.

We found no significant difference in growth rates between the sexes, although both Poole (1961) and Eldridge (1962) did report a significant difference. The growth rates probably are significantly different, an indication of this being the large difference in predicted maximum lengths from Walford's growth transformation (62 cm for males and 88 cm for females), but our limited sample size in older age-groups, particularly males, prevented this difference from being significant. The percent increase in annual length (Tables 2, 3) is similar for both sexes until age 6, and then it begins to decline more rapidly in males.

Our calculated growth rates underestimate those actually observed. Bigelow and Schroeder (1953) stated that the largest summer flounder for which they could find a definite record weighed 11,793 g (26 lb), and the largest fish recorded in sport fishing was 94 cm (37 in) long and weighed 9,072 g (20 lb). Using our predicted maximum lengths and length-weight relationship (see next section), we calculated that a male 62 cm (24.4 in) would weigh 2,339 g (5.21 lb) and a female 88 cm (34.7 in) would weigh 8,199 g (18.1 lb). Also our predicted length of 14 cm at age 1 (Y-axis intercept from Walford's growth transformation) is 3 cm smaller than the observed length given by Eldridge (1962). The lack of samples from age-group 1 and above age-group 8 and the limited samples in age-groups 6 through 8 might account for most of this error. A small change in the female growth rate would give a predicted maximum length of 98 cm, and then we have a fish weighing 11,793 g (26 lb). The growth rate of fish in age-groups 2 through 5 may approximate the growth of the same age-groups in the actual population.

LENGTH AND WEIGHT RELATIONSHIPS

A linear relationship existed between total length-standard length (Table 4), standard length-head length, and head length-upper jaw length. There were no significant differences in these relationships when the sexes are considered separately. The slope (3.151) of the line representing the total length-weight relationship (Table 4) was not significantly different from that (3.146) reported by Lux and Porter (1966) for summer flounder caught in June off Massachusetts. They found no difference between the slopes of the lines when sex was considered, but

TABLE 4.—Calculated values for regression equations describing the total length (TL in millimeters)-weight (W in grams) relationship and the total length (TL in millimeters)-standard length (SL in millimeters) relationship for summer flounder from Delaware Bay.

Number of fish	Sex	Intercept	Slope	Correlation coefficient	Standard error of estimate
		log W = log intercept + slope (log TL)			
[1]333	both	0.404×10^{-5}	3.151	0.995	0.095
102	male	0.102×10^{-4}	2.994	0.953	0.086
167	female	0.227×10^{-5}	3.246	0.987	0.086
		TL = intercept + slope (SL)			
314	both	16.695	1.155	0.986	4.035
102	male	11.044	1.173	0.994	3.531
168	female	18.861	1.150	0.998	4.351

[1]This includes 20 juveniles from North Carolina.

they stated that males were slightly heavier than females on an equal length basis. We found no real difference between the weights of equal sized males and females in Delaware Bay, nor did Eldridge (1962) for fish off Virginia. Twenty fish from North Carolina were included in our total length-weight relationship so we could have some data points from fish in age-groups 0 and 1.

GONAD DEVELOPMENT

Summer flounder gonads were examined from 1966 to 1968 for size and the ovaries for the presence of eggs. Gonads were small and flaccid from April through mid-August. From mid-August through November, the gonads began to enlarge or mature, and the ovaries contained eggs up to 0.4 mm in diameter. Murawski[4] stated that the size of mature eggs is 1.0 to 1.1 mm. There was never more than one-third of any catch during the fall with ripening gonads, and no mature fish were caught from December through March. We concluded that fish leave the bay as they ripen, supporting reports that summer flounder spawn after moving offshore during the winter. The smallest male taken with ripening testes was 30.5 cm, and the smallest female with ripening ovaries was 36 cm. These observations agree with those reported by Eldridge (1962) who stated summer flounder become sexually mature at age 3.

FOOD PREFERENCE

Stomachs from 131 flounder, ranging in size from 31 to 72.5 cm, were examined under a dissecting microscope, and 57% of them contained food. Food items found, listed in order of percent frequency of occurrence were: sand shrimp (*Crangon septemspinosa*, 41%), weakfish (*Cynoscion regalis*, 33%), mysid (*Neomysis americana*, 20%), anchovy (*Anchoa* sp., 7%), squid (*Loligo* sp., 4%), silverside (*Menidia menidia*, 1%), herring (*Alosa* sp., 1%), hermit crab (*Pagurus longicarpus*, 1%), and isopod (*Olencira praegustator*, 1%). On a volume basis weakfish were first, sand shrimp second, and the rest remained in the same order. Fish under 45 cm fed predominantly on invertebrates, while larger ones ate more fish. Poole (1964) found sand shrimp the primary organism eaten by summer flounder in Great South Bay, and that out of 10 fish species eaten, the winter flounder, *Pseudopleuronectes americanus*, was first by weight and the weakfish next to last. These observations indicate that the diet of summer flounder reflects local abundances of prey species.

Flounder caught during the day had a greater volume of food in their stomachs ($\bar{x}$ = 5.1 ml) than those caught at night ($\bar{x}$ = 3.3 ml), but the difference was not significant according to *t*-tests.

RACIAL ANALYSIS

The following morphometric and meristic characters were measured or counted on fish caught in 1966: total, standard, head, and upper jaw lengths; dorsal, anal, and pectoral fin rays; gill rakers on the first arch; and vertebrae (Table 5). All measurements and counts were made on the left side for uniformity. The number of caudal fin rays (17) and pyloric caeca (4) was constant so counting of these characters stopped after 20 fish. Woolcott et al. (1968) reported 18 caudal fin rays, with the posteriormost dorsal ray being very small and easily overlooked in unstained specimens. We missed this 18th ray in our count.

Ranges of some meristic and morphometric characters examined exceed those reported in the literature (Table 5). Analysis of variance showed no significant difference in the counts of the six variable meristic characters due to age or sex.

Comparison by *t*-test of meristic character counts on summer flounder sampled in Delaware Bay, Chesapeake Bay, and North Carolina (Table 6) gave inconclusive results. There was no significant difference between these areas for numbers of dorsal fin rays and vertebrae. Differences based on gill raker counts by Woolcott et al. (1968) might not be valid, because Deubler (1958) stated

[4]Murawski, W. S. 1966. Fluke investigations. N.J. Fed. Aid Proj. F-15-R-7 (Completion Rep. Job No. 3). N.J. Dep. Conserv. Econ. Dev., 24 p.

TABLE 5.—Meristic and morphometric data for summer flounder taken from Delaware Bay in 1966, and ranges reported in the literature that were exceeded.

Characters	Number of fish	Range	Mean	Standard error	Literature reported range
Meristic:					
Dorsal fin rays	194	80-98	88.92	0.20	[1]80-96
Anal fin rays	194	63-78	68.54	0.16	[2]60-73
Pectoral fin rays	196	10-13	11.83	0.05	[1]11-13
Gill rakers:					
Lower arch	196	14-19	16.31	0.08	
Upper arch	196	4- 7	5.59	0.05	
Vertebrae	195	40-43	41.34	0.04	[3]40-42
Morphometric:					
Standard length/head length	235	3.64- 4.30	3.96	0.01	[2,4] 3- 4
Head length/upper jaw length	235	1.54- 2.26	2.05	0.005	[2]2- 2.26

[1]Ginsburg (1952).
[2]Hildebrand and Schroeder (1928).
[3]Deubler (1958).
[4]Jordan and Evermann (1898).

TABLE 6.—A comparison of some summer flounder meristic characters between Delaware Bay (present study), Chesapeake Bay (Ginsburg 1952), and North Carolina [1 (Deubler 1958), 2 (Ginsburg 1952), and 3 (Woolcott et al. 1968)].

	Dorsal fin rays		Anal fin rays		Vertebrae		Gill rakers			
							Upper arch		Lower arch	
Location	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Delaware Bay	88.9	2.8	68.5	2.3	41.3	0.6	5.6	0.7	16.3	1.1
Chesapeake Bay	88.6	2.6	68.6	2.3			5.6	0.6	16.5	0.9
N.C. (1)	89.0	2.7	68.4	2.6	41.3	0.5				
N.C. (2)	88.1	2.7	67.7	2.2			5.0	0.7	15.6	1.3
N.C. (3)	88.4	1.4	68.3	1.2	41.2	0.6	5.2	1.0	14.6	1.5

	Anal fin rays					Gill rakers: Upper arch				Gill rakers: Lower arch			
Location	Del. Bay	Ches. Bay	N.C. (1)	N.C. (2)	N.C. (3)	Del. Bay	Ches. Bay	N.C. (2)	N.C. (3)	Del. Bay	Ches. Bay	N.C. (2)	N.C. (3)
Delaware Bay				*				**				**	**
Chesapeake Bay				*				**				**	**
N.C. (1)													
N.C. (2)	*	*				**	**			**	**		*
N.C. (3)										**	**	*	

* = significant difference at 0.05 level.
** = significant difference at 0.01 level.

the definitive number of gill rakers is not usually present until summer flounder are 18 mm standard length. Woolcott et al. used fish below this length, and this could account for the significant difference between their counts of lower arch gill rakers and the counts by Ginsburg (1952), also for fish from North Carolina.

Anal fin and gill raker data (Table 6) do suggest, however, that summer flounder from North Carolina belong to a population that is racially different from the population containing Chesapeake Bay and Delaware Bay flounder. This supports Smith's (1973) observation that there is mounting evidence for the existence of separate populations of summer flounder based on: 1) distribution of eggs and larvae, 2) meristic differences, 3) tag returns, and 4) commercial flounder landings. It is possible that separate populations or stocks exist because summer flounder undergo fairly rapid development, 74 to 94 h hatching time (Smith 1973), and conditions affecting egg and larval transport may minimize mixing between geographic areas. This possibility is suggested by Chang and Pacheco (1976) even though they assumed a unit stock for their population evaluation. There should be more research into the possibility of multiple populations before final management recommendations are made.

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LARVAL DEVELOPMENT OF THE SPIDER CRAB, *LIBINIA EMARGINATA* (MAJIDAE)[1]

D. MICHAEL JOHNS[2] AND WILLIAM H. LANG[3]

ABSTRACT

Larval development of the spider crab, *Libinia emarginata*, consists of two zoeal stages and megalopa. Laboratory-reared larvae (South Carolina and Rhode Island) are described and compared with planktonic larvae from Narragansett Bay, R.I. No significant variations in morphology were found between laboratory-cultured larvae and "wild" larvae from plankton catches; first stage zoea from South Carolina were smaller than Rhode Island specimens. Using *Artemia* diets, the best percentage survival in culture was found to be 20°C for Rhode Island larvae and 25°C for South Carolina larvae. Zoeal stages show little difference from larvae of *L. dubia*; however, the megalopae of the two species can be differentiated by the number of protuberances on the cardiac region of the carapace.

Larval stages have previously been described for a number of species from the family Majidae (Sandifer and Van Engel 1971, 1972). For the genus *Libinia* only two complete descriptions have been published. Boschi and Scelzo (1968) described larval stages of *L. spinosa* from Mar del Plata Harbor, Argentina; and Sandifer and Van Engel (1971) described the larval stages of *L. dubia* from Chesapeake Bay. Larvae of *L. erinacea* have been described by Yang (1967), but the results remain unpublished. In all cases, the larval development consists of two zoeal stages and a megalopa.

Adult *Libinia emarginata* Leach range from Windsor, Nova Scotia, to the western Gulf of Mexico and are found in nearshore waters down to a depth of 29 m (Williams 1965). Although the larvae of *L. emarginata* have not been formally described, they have been successfully reared (J. D. Costlow, pers. commun.). Grassle (1968) studied heterogeneity of hemocyanins during ontogeny, but no attempt was made to describe development. In support of ongoing studies using *Libinia* larvae at this laboratory, the present study was undertaken to: 1) describe the larval stages, 2) compare morphology of laboratory cultured and field collected larvae, and 3) determine successful temperature-salinity rearing parameters and development times. Characteristics which distinguish *L. emarginata* larvae from the larvae of *L. dubia* and *L. erinacea* were also noted.

METHODS AND MATERIALS

Ovigerous females of *L. emarginata* were collected off Charleston, S.C., during fall 1975 and spring 1976, and in Narragansett Bay, R.I., during summer 1976. Females were isolated in chambers at 25°C (in South Carolina) or 20°-22°C (in Rhode Island) and 30‰. After hatching, zoeae were isolated into compartmentalized plastic boxes. Larvae were fed day old *Artemia* every other day following a change of water. Larvae reared at salinities other than 30‰ were brought to the appropriate levels (15, 20, 40, or 45‰) using increment changes of 2.5‰ every 30 min. Larvae reared at temperatures other than hatching temperature were brought to the test temperature (15°, 20°, or 30°C) by placing larvae in environmental chambers and allowing them to equilibrate to these temperatures.

Field samples were obtained from surface plankton tows collected in Narragansett Bay during July and August 1976.

Drawings were made with the aid of camera lucida using exuviae and larvae fixed in 10% Formalin.[4] Carapace and total lengths were made with an ocular micrometer. Dry weights were determined with a Cahn Electrobalance on larvae

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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that were dried in an 80°C oven for 24 h. The weights for each stage were calculated from three samples of five zoeae each.

One-way analysis of variance was computed on carapace length measurements taken on larval stages from South Carolina reared, Rhode Island reared, and field samples. If significant differences (at $P = 0.05$) were found within stages, a Scheffe Posterior comparison was used to determine where the differences lay (Nie et al. 1975).

The following abbreviations were used in all descriptions: AN1 = antennule, AN2 = antenna, MN = mandible, MAX1 = maxillule, MAX2 = maxilla, MXP1 = first maxilliped, MXP2 = second maxilliped, MXP3 = third maxilliped, P1 to P5 = pereopods 1 to 5, PL2 to PL6 = pleopods on abdominal somites 2 to 6. Types of setae specified are as described by Bookhout and Costlow (1974).

RESULTS

Development

Development times in both the South Carolina and Rhode Island reared larvae vary with temperature and salinity. In the South Carolina larvae, optimal and most advanced development occurred at 25°C and 30‰. At these conditions, the second stage appeared at day 3, megalopa at day 6 and first crab at day 14. In other conditions tested, development did not continue past the megalopa (Table 1).

In the Rhode Island reared larvae, complete development occurred only at 20°C and 30‰ with the second zoeal stage appearing at day 5, megalopa at day 8, and first crab at day 14. With other conditions tested, development was varied (Table 1).

TABLE 1.—Time to various developmental stages (in days) for the spider crab, *Libinia emarginata*, reared at various temperature-salinity combinations in both South Carolina and Rhode Island.

Rearing site	Temperature-salinity combination	No. of larvae	Stage		
			II	Megalopa	1st crab
South Carolina	15°C-30‰	36	12	27	(1)
	20°C-30‰	36	7	12	(1)
	25°C-15‰	54	(1)		
	25°C-20‰	54	3	8	(1)
	25°C-30‰	54	3	6	14
	25°C-40‰	54	3	7	(1)
	25°C-45‰	54	4	8	(1)
	30°C-30‰	36	(1)		
Rhode Island	15°C-30‰	60	(2)		
	20°C-30‰	60	5	8	14
	25°C-30‰	60	4	(1)	

[1]All larvae had died prior to this stage.
[2]Second stage was not reached by day 15.

South Carolina reared larvae tended to be smaller than both Rhode Island reared and field samples (Table 2). With statistical analysis, this difference is significant in stage I ($P < 0.05$) but only between South Carolina reared and Rhode Island reared. At no other stage were the size variations found to be significant.

TABLE 2.—Comparison of carapace lengths for South Carolina reared, Rhode Island reared, and field sample larvae of *Libinia emarginata*.

Stage	Item	South Carolina reared	Rhode Island reared	Field samples
Zoea I*	$\bar{x}$ (mm)	[1]0.75	[1]0.78	0.775
	SD (mm)	0.019	0.020	0.028
	N	10	10	13
Zoea II	$\bar{x}$ (mm)	0.94	0.94	0.96
	SD (mm)	0.02	0.038	0.035
	N	7	14	11
Megalopa	$\bar{x}$ (mm)	1.16	1.21	1.20
	SD (mm)	0.049	0.064	0.001
	N	4	3	4

*Indicates significant differences within a stage by one-way analysis of variance ($P = 0.05$).
[1]Significant differences exist between the two means, according to Scheffe's Posterior comparison.

Larval Description

Two zoeal stages and one megalopa were obtained during the rearing period. Mandibles of the zoea are without palps and have a complex triangular biting surface. Since, in these stages, mandibles appear to have little diagnostic value and are difficult to accurately portray, they have been omitted from the following description.

Zoea I

Size and weight—Average carapace length, 0.78 mm (range 0.76-0.80 mm), average total length 2.19 mm (range 2.00-2.30 mm). Average dry weight 0.0214 mg (range 0.0200-0.0224 mg).

Carapace (Figure 1A, B) with dorsal and rostral spines; lateral spines absent. Dorsal spine long and slightly curved posteriorly; rostral spine nearly as long as antennule and slightly curved inward. Carapace large and somewhat rounded; 7 small plumose setae along the ventrolateral margin of carapace. Eyes sessile.

Abdomen (Figure 1C) with 5 somites; 6th somite fused to telson. Somite 2 with small anteriorly curved knobs on each side of lateral surface; somites 3-5 with pair of small posterolateral spines. Bifurcate telson; each furca bearing 1 spine. Inner

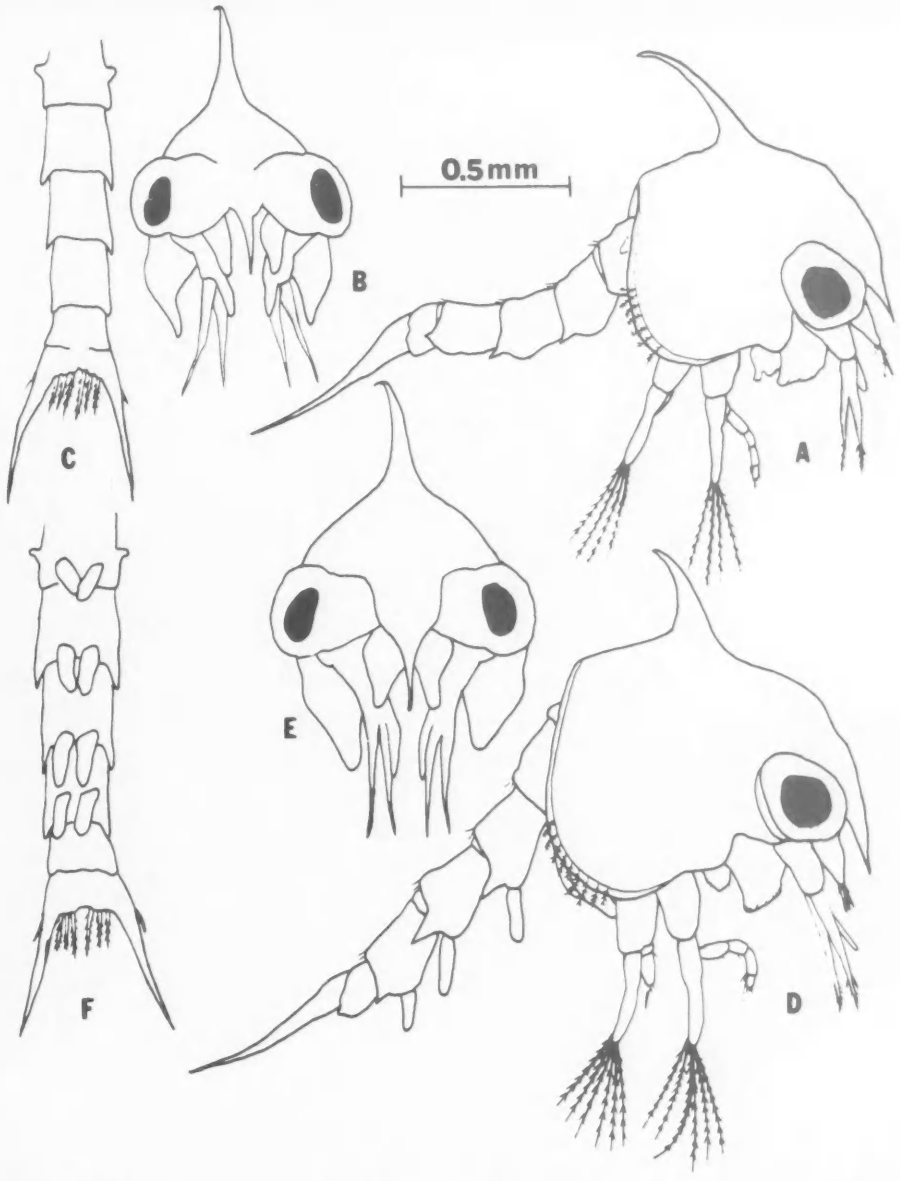

FIGURE 1.—*Libinia emarginata* zoea I and II. (A) lateral view of stage I, (B) front view of stage I, (C) dorsal view of abdomen at stage I, (D) lateral view of stage II, (E) front view of stage II, (F) dorsal view of abdomen at stage II. All unmarked scales = 0.1 mm.

margin of telson fork bearing 6 spines of approximately the same length.

AN1 (Figure 2C)—Uniramous, unsegmented, and conical with 2 long aesthetascs, 2 smaller aesthetascs, and one simple setae on the terminal end.

AN2 (Figure 2D)—Protopodite long, ending in a point with 2 rows of spinules distally, small endopodite bud near base. Exopodite long, spinulose distally; 2 small spines just subterminal, innermost spinulose.

MAX1 (Figure 2F)—Endopodite 2-segmented; proximal segment with 1 long simple or sparsely plumose seta, distal segment with 4 terminal setae (2 plumose, 2 plumodenticulate) and 1 subterminal plumose seta. Basal endite with 4 plumodenticulate cuspidate and 2 plumodenticulate terminal setae and 1 subterminal plumose seta; smaller coxal endite with 5 plumose setae and 2 simple setae.

MAX2 (Figure 2E)—Scaphognathite with 9 plumose marginal setae and a plumose apical tip. Endopodite simple with 4 (rarely 5) terminal plumodenticulate setae and 1 simple seta. Basal endite slightly bilobed; 4-5 plumodenticulate setae on distal lobe and 5 (rarely 4) plumodenticulate setae on proximal lobe. Coxal endite bilobed; 3-4 plumose setae on distal lobe and 4 plumose setae on proximal lobe.

MXP1 (Figure 2A)—Exopodite with 4 long, plumose natatory setae. Endopodite 5-segmented; setation formulae (proximal to distal): 3, 2, 1, 2, 5. Terminal segment with 5 setae (4 multidenticulate and 1 short, simple). Basiopodite with up to 9 setae.

MXP2 (Figure 2B)—Exopodite with 4 plumose

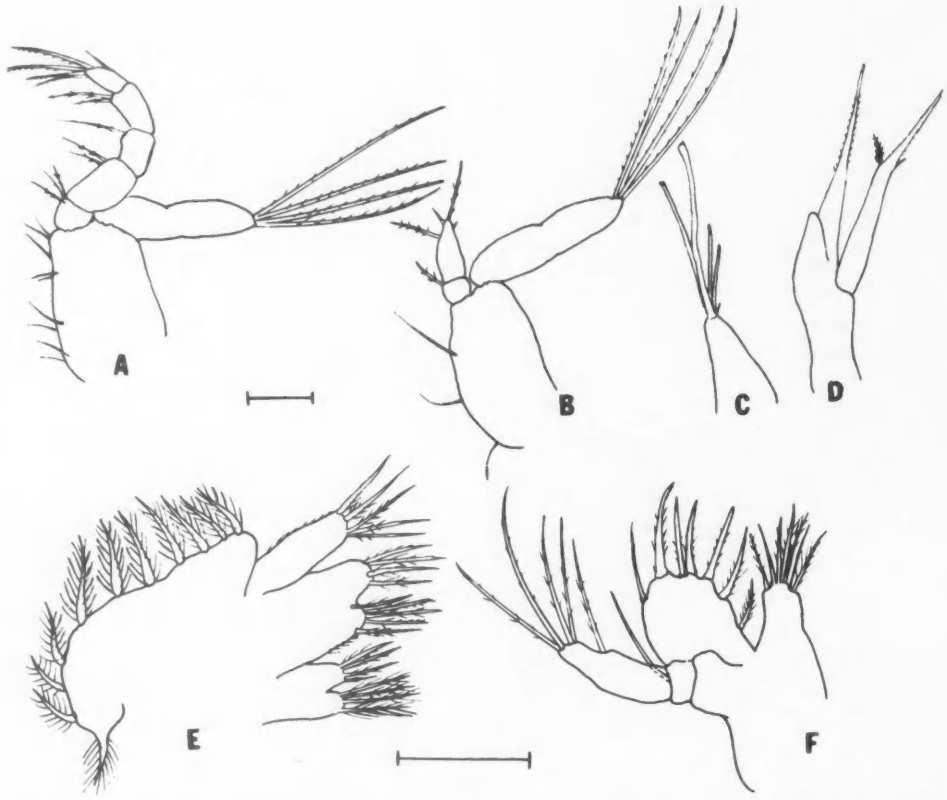

FIGURE 2.—*Libinia emarginata*. Appendages of stage I zoea. (A) first maxilliped, (B) second maxilliped, (C) antennule, (D) antenna, (E) maxilla, (F) maxillule. All unmarked scales = 0.1 mm.

natatory setae. Endopodite 2-segmented; terminal segment with 4 setae (2 plumodenticulate and 2 simple). Basiopodite with 3 setae.

Zoea II

Size and weight—Average carapace length, 0.94 mm (range 0.89-0.98 mm), average total length 2.69 mm (range 2.56-2.82 mm). Average dry weight, 0.0654 mg (range 0.0613-0.0712 mg).

Carapace (Figure 1D) same as for stage I. Dorsal spine proportionately shorter and stouter than before. Ventrolateral margin now with 8-10 small plumose setae. Eyes stalked.

Abdomen (Figure 1F) with 6 somites. Somite 2 with small anteriorly curved knobs as before. Somites 2-5 with 2 pleopod buds ventrally. Telson as in stage I.

AN1 (Figure 3C)—With 2 long, thick aesthetascs, 4 smaller aesthetascs, and 1-2 simple setae or thin aesthetascs on terminal end.

AN2 (Figure 3D)—Protopodite same as before, endopodite bud at least half length of protopodite. Exopodite same as before.

MAX1 (Figure 3F)—Endopodite same as before. Basal endite with 8 terminal setae (5 denticulate cuspidate and 3 plumodenticulate), and 2 subterminal plumose setae; coxal endite with 8 setae (5 plumose and 3 simple).

MAX2 (Figure 3E)—Scaphognathite with 16 (in South Carolina reared) or 20 (in Rhode Island reared and field samples) plumose marginal setae. Endopodite with basal endite and coxal endite same as in stage I.

MXP1 (Figure 3A)—Exopodite with 6 large plumose natatory setae. Endopodite same as before. Basiopodite with up to 10 setae.

MXP2 (Figure 3B)—Exopodite with 6 large,

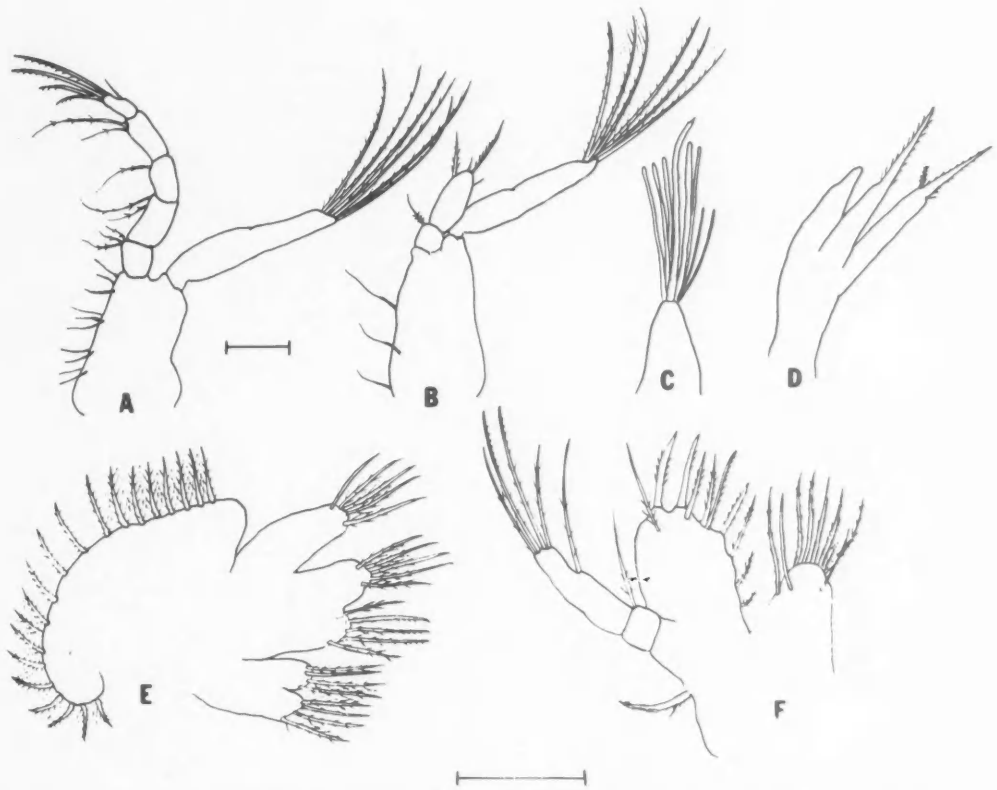

FIGURE 3.—*Libinia emarginata*. Appendages of stage II zoea. (A) first maxilliped, (B) second maxilliped, (C) antennule, (D) antenna, (E) maxilla, (F) maxillule. All unmarked scales = 0.1 mm.

plumose natatory setae. Endopodite and basiopodite same as before.

Megalopa

Size and weight—Average carapace length, 1.21 mm (range 1.16-1.28 mm), average total length 2.14 mm (range 2.07-2.17 mm). Average dry weight 0.205 mg (range 0.145-0.259 mg).

Carapace (Figure 4A, B) without spines; short rostrum tapers to blunt tip. Median line of carapace depressed between eyes with 2 partially connected protuberances along gastric region, paired protuberances at cardiac region and slight protuberance at posterior border. Lateral carapace region with 3 paired protuberances, surface somewhat expanded over posterolateral area.

Abdomen (Figure 4B) with 6 somites plus telson.

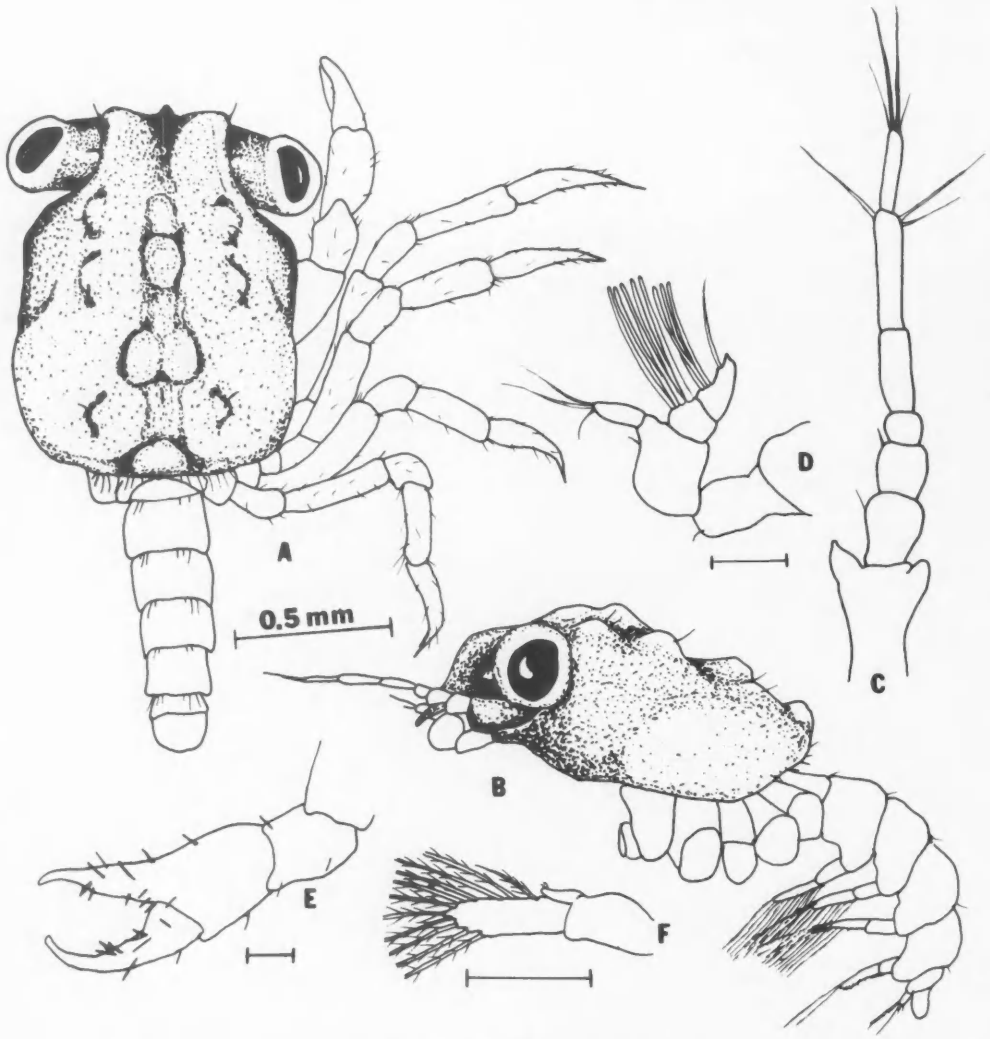

FIGURE 4.—*Libinia emarginata* megalopa. (A) dorsal view, (B) lateral view, (C) antenna, (D) antennule, (E) cheliped, (F) pleopod. All unmarked scales = 0.1 mm.

AN1 (Figure 4D)—Peduncles 3-segmented; basal segment bare, second and third segment with 1 short seta each. Inner flagellum unsegmented with 3 terminal simple setae; dorsal flagellum 2-segmented proximal segment with 5 aesthetascs; distal with 3 aesthetascs and 1 subterminal simple seta.

AN2 (Figure 4C)—Peduncle 3-segmented. Flagellum 4-segmented, with 2 distal segments having 3 subterminal and 4 terminal simple setae, respectively.

MN (Figure 5A)—Palp 3-segmented with 5 terminal setose setae.

MAX1 (Figure 5B)—Endopodite unsegmented with 2-3 terminal simple setae. Basal endite with 14 processes (6 plumodenticulate cuspidate, 6 plumodenticulate, 2 short multidenticulate) and 2-3 marginal plumose setae; coxal endite with 3 plumodenticulate and 3 simple terminal setae and 4 subterminal plumose setae.

MAX2 (Figure 5C)—Scaphognathite with 31-33 (in South Carolina reared) or 33-35 (in Rhode Island reared and field samples) plumose marginal setae. Endopodite with 0-1 seta. Basal endite bilobed; distal portion and proximal portion with 6-7 plumodenticulate or plumose setae each. Coxal endite bilobed; distal portion with 3 plumose setae and proximal portion with 4 plumose and 1 simple setae.

MXP1 (Figure 5D)—Exopodite 2-segmented, proximal segment with 1 plumose seta; distal segment with 5 plumose and 1 simple setae. Endopodite unsegmented with 1-3 terminal setae. Basal endite with 8-10 plumodenticulate setae; coxal endite with 6 plumodenticulate and 1 plumose setae. Epipodite with 4 long simple setae.

MXP2 (Figure 5E)—Exopodite 2-segmented; distal segment with 5-6 long plumose setae. Endopodite 4-segmented; setation formulae (proximal to distal) 0, 1, 3, 6. Distal setae, 5 plumodenticulate cuspidate, 1 simple.

MXP3 (Figure 5F)—Exopodite 2-segmented; terminal segment with 3-4 long plumose and 2 small simple terminal setae. Endopodite 5-segmented; setation formulae (proximal to distal) 9-10, 7-8, 4, 6, 4, mostly plumodenticulate or serrate plumose setae. Epipodite with 3 terminal and 3 subterminal multidenticulate setae.

P1 to P5 (Figure 4A, E)—Moderately setose, cheliped similar to adult form.

PL2 to PL6 (Figure 4F)—Exopodite 2-segmented; plumose natatory setae on distal segment varies from 11 (PL2) to 8 (PL5). Endopodite small with 2 small hooks.

Zoeal Chromatophores

Libinia emarginata larvae are sparsely pigmented in freshly sacrificed specimens. Chromatophore color ranges from orange to a dark brown-red. Distinctive pigment areas with little individual variation include an orange spot at the posterior dorsal spine base, a deep red area posterior to the eye base, a large distinctive red spot on the posterolateral carapace region near the carapace setae and red pigmentation of the mandibles. The abdomen is pigmented in the central ventral area of each segment juncture. Additional pigment spots occur on the carapace and appendages but do not appear consistent in location or occurrence.

DISCUSSION

There is only a narrow range of temperature-salinity conditions at which the larvae successfully develop in the laboratory. With South Carolina larvae, these conditions are 25°C and 30‰, while with Rhode Island larvae, maximum development occurs at 20°C and 30‰. The difference in these temperatures possibly reflects the influence of latitudinal separation on larval development, however, until critical experiments are undertaken, this cannot be confirmed (Vernberg 1962; Vernberg and Costlow 1966; Sastry 1970; Sastry and Vargo 1977). The larvae develop best in temperatures that represent the mean temperature during the larval season. Gravid *L. emarginata* were collected from May to September in South Carolina in coastal waters that had a mean water temperature near 25°C. In Rhode Island, gravid crabs were collected from July to August in bay and coastal waters that had a mean water temperature near 20°C.

The narrowness of successful rearing conditions may reflect inadequate rearing variables such as diet, substrate, water circulation, etc. (Roberts 1972; Sulkin 1975; Sulkin and Norman 1976), or reflect the habitat of *L. emarginata*. With larvae that develop entirely in bay or coastal waters, there follows a characteristic inability of larvae to develop successfully over wide ranges of temperature and salinity, while larvae from estuarine waters usually develop in a much wider range of temperatures and salinity. In the offshore

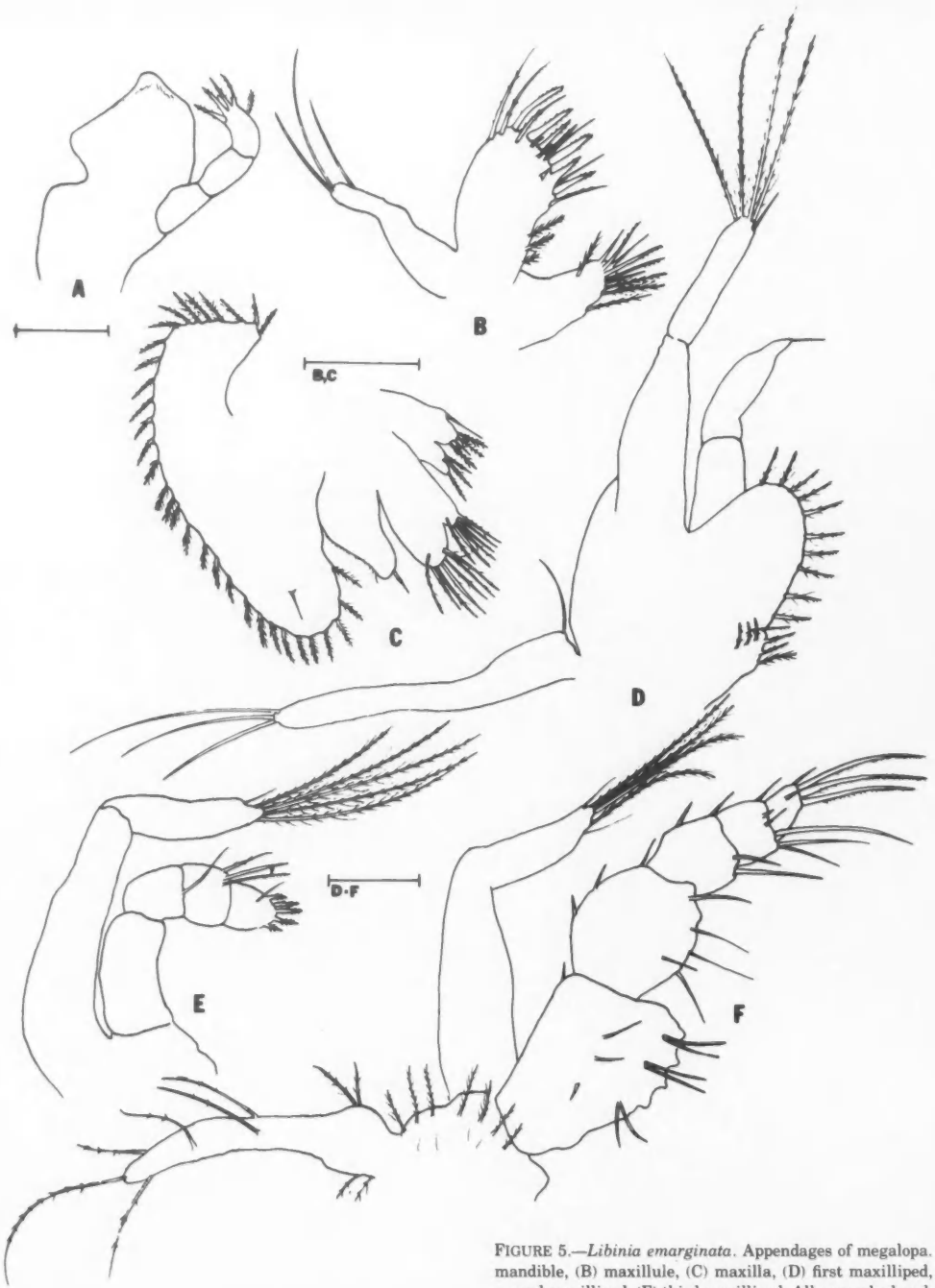

FIGURE 5.—*Libinia emarginata*. Appendages of megalopa. (A) mandible, (B) maxillule, (C) maxilla, (D) first maxilliped, (E) second maxilliped, (F) third maxilliped. All unmarked scales = 0.1 mm.

spawner, *Callinectes sapidus*, for example, larvae will complete early development only at 25°C and 31.1‰ (Costlow and Bookhout 1959) while an estuarine xanthid, *Rhithropanopeus harrisii*, completes development at temperatures of 20°, 25°, and 30°C and salinities between 2.5 and 40‰ (Costlow et al. 1966). Throughout this study, all gravid females were collected in near coast bay or open coastal waters (>30‰ salinity).

The duration of development within the genus *Libinia* also varies. Boschi and Scelzo (1968) reported that development for *L. spinosa* required 20-30 days (at 20°C) or an average of 8-10 days per stage. *Libinia erinacea* required 14 days (at 20°C) or 9 days (at 25°C) to reach first crab stage (Yang 1967). Sandifer and Van Engel (1971) reported that *L. dubia* needed only 9 days (at 25.5°-28.5°C) for larval development. *Libinia emarginata* is intermediate with at least 14 days needed to reach first crab stage. As pointed out by Sandifer and Van Engel (1971), these differences in development times may be explained, in part, by rearing temperatures. For *L. erinacea*, total development time is reduced by 5 days with a 5°C increase in temperature. However, other factors must also play a role in development for *L. spinosa* and *L. erinacea* reared at the same temperature (20°C) and given the same food source (*Artemia*) still showed a 6- to 16-day difference in development times.

The number of larval stages for *L. emarginata* is typical for the family Majidae (Gurney 1942; Hart 1960). Larvae from the three sources examined showed few differences. South Carolina larvae tended to be slightly smaller than Rhode Island and field samples (Table 2). Morphology of larvae was virtually identical in all cases, except for the scaphognathite setal number being consistently lower in South Carolina larvae. In this case, reared larvae appear to represent accurate "mimics" of wild larvae, even to specific setal types. However, it is unknown if this similarity also pertains to physiological or behavioral parameters.

In comparing larval descriptions of *L. erinacea*, *L. dubia*, *L. spinosa*, and *L. emarginata*, we have found that carapace setation and armature of the abdominal somites are the most useful zoeal characters (Table 3). *Libinia erinacea* and *L. spinosa* may be distinguished by the presence of lateral spines on abdominal somite 2, as opposed to small knobs for *L. dubia* and *L. emarginata*. *Libinia spinosa* may be differentiated from *L. erinacea* by the lack of setation on the ventrolateral margin of the carapace. The first zoea of *L. dubia* and *L. emarginata* show no differences in general morphology and setal numbers. The second zoea of *L. emarginata* usually has 10 setae on the ventrolateral margin while *L. dubia* has 8 setae but as in stage I there appears to be no ready

TABLE 3.—Comparison of diagnostic characteristics for zoeal stages of *Libinia erinacea*, *L. spinosa*, *L. dubia*, and *L. emarginata*.

Species and stage	Dorsal spine	Abdominal somites		Carapace setation
		Somite 2	Somites 3-5	
L. erinacea:[1]				
Zoea I	Single, long, curved posteriorly, sometimes ending in short hook	Two lateral spines, one on each side, pointing posteriorly	Two medium spines, one on each side, pointing posteriorly	6 setae on ventrolateral margin
Zoea II	Same as zoea I	Same as in zoea I, but with pair of pleopod buds per somite	Same as in zoea I, but with pair of pleopod buds per somite	8 setae on ventrolateral margin
L. spinosa:[2]				
Zoea I	Same as in *L. erinacea*	Same as in *L. erinacea*	Two long spines, one on each side, pointing posteriorly	No setation on ventrolateral margin
Zoea II	Same as in *L. erinacea*	Same as in *L. erinacea*	Same as in zoea I, but with pair of pleopod buds per somite	No setation on ventrolateral margin
L. dubia:[3]				
Zoea I	Single, fairly long, curved posteriorly	Two small curved knobs, one on each side	Two small spines, one on each side, pointing posteriorly	6-7 setae on ventrolateral margin
Zoea II	Same as zoea I	Same as in zoea I, but with pair of pleopod buds per somite	Same as in zoea I, but with pair of pleopod buds per somite	7-8 setae on ventrolateral margin
L. emarginata				
Zoea I	Single, long, slightly curved posteriorly	Same as in *L. dubia*	Same as in *L. dubia*	7 setae on ventrolateral margin
Zoea II	Short and stout	Same as in *L. dubia*	Same as in *L. dubia*	8-10 setae on ventrolateral margin

[1]From Yang (1967).
[2]From Boschi and Scelzo (1968).
[3]From Sandifer and Van Engel (1971).

TABLE 4.—Average carapace lengths, total lengths and dry weights for the larval stages of *Libinia emarginata*, *L. dubia*, *L. erinacea*, and *L. spinosa*.

Species	Carapace length (mm)			Total length (mm)			Dry weight (mg)		
	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa	Zoea I	Zoea II	Megalopa
L. emarginata	0.78	0.94	1.21	2.19	2.69	2.14	0.0214	0.0654	0.205
L. dubia[1]	0.81	0.97	1.16	2.35	2.78	2.11	—	—	—
L. erinacea[2]	0.88	1.03	1.24	—	—	—	—	—	—
L. spinosa[3]	0.80	0.96	1.30	2.30	2.80	3.10	—	—	—

[1]From Sandifer and Van Engel (1971).
[2]From Yang (1967).
[3]From Boschi and Scelzo (1968).

means to distinguish the species. *Libinia dubia* zoea, as described by Sandifer and Van Engel (1971), are larger than *L. emarginata* zoea (Table 4), but statistical analysis of various samples would be needed to determine if a consistent size difference exists. Differences in setal types may also occur, but these have not been described for *L. dubia*. As with larvae of various species of *Uca* (Hyman 1920), a rapid, reliable means to distinguish *L. emarginata* and *L. dubia* larvae to species does not exist.

Megalopae of all four species, however, are distinguishable. *Libinia spinosa* has a distinct dorsal spine which curves posteriorly (Boschi and Scelzo 1968) while the dorsal spine of *L. erinacea* is long and upright (Yang 1967). *Libinia dubia* and *L. emarginata* megalopae both lack a dorsal spine. The median cardiac protuberance of the *L. dubia* megalopa is single but is paired in *L. emarginata*. This difference is relatively easy to observe, thus unlike zoeal stages, *L. dubia* and *L. emarginata* megalopae may be identified to species.

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THE RIBBONFISH GENUS *DESMODEMA*, WITH THE DESCRIPTION OF A NEW SPECIES (PISCES, TRACHIPTERIDAE)

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ABSTRACT

The genus *Desmodema* is unique within the Trachipteridae in that the upper caudal lobe, borne on the second ural centrum, is not upturned, and the lower caudal lobe, borne on the first ural centrum in other trachipterids, is absent, and in that there are seven dorsal pterygiophores before the first neural spine. *Desmodema lorum* n.sp. can be distinguished from *D. polystictum* (Ogilby) on the basis of having more vertebrae, fewer caudal rays, a longer tail, and the snout longer than the eye diameter. *Desmodema polystictum* is probably circumtropical; *D. lorum* is restricted to the North Pacific Ocean. The species of *Desmodema* have a distinctive prejuvenile phase characterized by polka dots on the sides, long pelvic fins, a relatively short tail, and elongation of the first six dorsal rays. Metamorphosis is abrupt and involves loss of the pelvic fins, elongated dorsal rays and polka dots, and a great lengthening of the tail. It is suggested that metamorphosis accompanies movement to a deeper habitat. The elongated tail is related to extension of the lateral-line sensory system. On the basis of joint possession of a dermal tubercle and pore system and an abruptly constricted body, *Desmodema* and *Zu* are regarded as related. *Desmodema*, but not *Zu*, agrees with *Regalecus* in the arrangement of the dorsal pterygiophores.

The genus *Desmodema* was erected for the reception of *Trachypterus jacksoniensis polystictus* Ogilby (Walters and Fitch 1960). Fitch (1964) subsequently redescribed *Desmodema polystictum*, mainly utilizing material from the northeast Pacific, and placed *Trachypterus misakiensis* Tanaka, 1908 and *T. deltoideus* Clark, 1938 in its synonymy. Our interest arose from the observation that two recently collected specimens had what appeared to be anomalously low vertebral counts. This initiated the present study, which has revealed the existence of two species, one of them undescribed. In addition to distinguishing and describing the species, our material has allowed us to amplify the generic description of *Desmodema* and to detail some of the remarkable ontogenetic changes undergone by its species.

MATERIALS AND METHODS

Specimens used in this study are housed in the following institutions: California Academy of Sciences (CAS), Department of Biology, University of California, Los Angeles (UCLA), Natural History Museum of Los Angeles County (LACM), and Scripps Institution of Oceanography (SIO). In the material list the first length measurement is the snout-vent length (SV), the second the standard length (SL). A single value indicates snout-vent length of a broken specimen.

Because of the delicacy of the species, most of the specimens were damaged in some way, and not all counts and measurements were made on all specimens. In particular, fin lengths represent minimum measurements, since all fins seem to have been broken to some degree. No specimen appeared to have unbroken pelvic fins. Measurements are self-explanatory and were taken with flat-point dividers or dial calipers. Vertebral counts were taken from radiographs or cleared and stained material. Dorsal rays could be enumerated on only a few specimens.

RESULTS

Desmodema Walters and Fitch

Desmodema Walters and Fitch 1960. Type-species *Trachypterus jacksoniensis polystictus* Ogilby 1897, by original designation.

Diagnosis.—A trachipterid with 4-10 caudal rays, the caudal on the same axis as the caudal peduncle, all caudal rays borne on terminal centrum, no lower caudal lobe. Seven dorsal pterygiophores before first neural spine. Body con-

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stricted behind anus, tail exceedingly elongated in juveniles and adults. Young with numerous dark round spots. Skin of adults pierced by numerous pores.

Description—Body strongly compressed laterally, postanal portion of body narrowing into a whiplike tail in juveniles and adults (posterior vertebrae about four times as long as 14th vertebra). Posterior region of body of larvae and prejuveniles narrow, but not exceedingly elongate (posterior vertebrae shorter than 14th vertebra). Seven pterygiophores before first neural spine, one or two pterygiophores between first and second neural spines. First pterygiophore closely applies to back of skull, no predorsal bones. Anterior five or six dorsal rays elongated in larvae and prejuveniles to form a dorsal pennant; these rays completely lost in adults. Pelvics long and fanlike in young, absent in adults. Caudal well developed, of 4-10 unbranched rays, parallel to axis of tail. Caudal rays all borne on last ural centrum, no ventral caudal lobe (Figure 1).

Fin rays with a lateral row of small spines, these weak or absent on posterior pelvic rays, middle caudal rays, and pectoral rays. Each dorsal ray anterior to elongated tail portion of body with a single laterally directed stout spine on either side of the base.

Lateral line ending at caudal base, lateral-line scales with a pair of spines. Body otherwise scaleless at all sizes (*D. polystictum*), or young covered with scales, each with a pair of longitudinal spinous ridges (*D. lorum*). Skin of adults with cartilaginous tubercles, and pierced by numerous pores (Walters 1963). No enlarged tubercles on ventral midline.

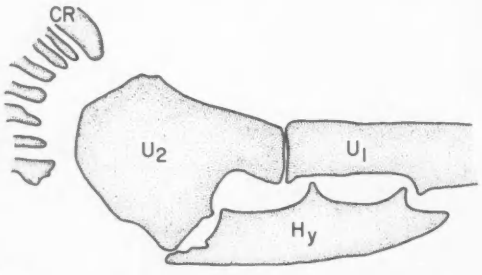

FIGURE 1.—Caudal skeleton of *Desmodema polystictum*, SIO 73-340. Camera lucida drawing at 25× magnification. Only bases of caudal rays shown. CR, caudal ray; Hy hypural; U_1, first ural centrum; U_2, second ural centrum and hypural.

Two nostrils in prejuveniles, the posterior just before anterior margin of eye; posterior opening obliterated in juveniles and adults. Nasal epithelium without ridges or folds at all sizes. Head bones cancellous and ridged. Mouth strongly oblique. Teeth restricted to one to four in each premaxilla and two enlarged, recurved fangs on mandible, one on either side of symphysis. Gill rakers (2-3) + (9-10) usually 3 + 9, fleshy, distally expanded and leaflike. Rakers of upper limb with a few teeth. Pseudobranch well developed. Gas bladder present in small juveniles (to about 30 mm SV), rudimentary or absent in large juveniles and adults.

Very young silvery, prejuveniles silvery with profuse dark spotting, adults without spots.

Growth changes.—Although we have no material smaller than 18.9 mm SV, it appears that development from a silvery or transparent form with a triangular outline with the head deepest, into the polka-dotted, deep bodied prejuvenile is gradual. The transition from prejuvenile to juvenile is probably rapid and can fairly be termed a metamorphosis. There is a large-size gap in our material of *D. polystictum* (91-260 mm SV), but our material of *D. lorum* includes the appropriate size classes. The difference between the prejuvenile and the final body form can be seen in Figure 5. The two specimens are almost identical in snout-vent length. However, the upper specimen is essentially a miniature adult. The major differences are in the change in the ventral profile, elongation of the tail, increase in eye size, eruption of lower jaw teeth, and loss of the spots, pelvic fins, and posterior nostril. Juveniles, including our largest (173 mm SV) have an elongate opening not yet covered over by the skin at the position of the pelvic fins, indicating that loss of the pelvics may be rapid, and from the base.

Walters (1963) indicated that juveniles of *D. polystictum* are scaled, but that adults are scaleless, and have cartilaginous tubercles and a subdermal canal system connected to the surface by numerous pores. In our material of *D. lorum* an 18.5-mm SV silvery individual lacks both scales and tubercles. An individual 36 mm SV is scaled, but lacks tubercles, and in another (36.5 mm SV), tubercles are present ventrally, and on the sides behind the head. Our largest polka-dotted prejuvenile is 95 mm SV. The upper sides are scaled; the remainder of the body is covered with tubercles and the subcutaneous canal system is well

developed, with surface pores present. A juvenile of 104 mm SV has scales along the dorsal base, and one of 131 mm SV lacks scales and has tubercles and pores over the entire body.

Desmodema polystictum does not agree with *D. lorum* in the course of development of the tubercles and pore system. None of our specimens has scales. Instead tubercles are developed in a specimen of 36 mm SV, and tubercles and pores are present in an individual of 42 mm SV. Walters (1963) was unaware of the existence of the two species of *Desmodema* and his figure 1 was undoubtedly based on a juvenile of *D. lorum*.

In juveniles the first six dorsal rays are elongated (broken in all our specimens). These rays, which are borne on the pterygiophores before the first neural spine, are lost, and in adults represented by a stiffening in the skin. The recurved, fanglike lower jaw teeth first appear at a snout-vent length of about 100 mm.

Life history and behavior.—We lack data from closing nets, and thus have no precise information on depth of capture of our material. Fitch and Lavenberg (1968) inferred that *Desmodema "polystictum"* lives "500 to 1,000 feet beneath the sea's surface" and Walters (1963) predicated his discussion of energetics on the assumption that *Desmodema* is mesopelagic. Harrison and Palmer (1968) speculated that *Desmodema*, which they described as "chocolate brown," might live deeper than its silvery relatives. Actually *Desmodema* is silvery and turns brown in preservative.

The number of polka-dotted juveniles of *D. polystictum* taken at or near the surface indicates that they probably mainly occupy the euphotic zone. The polka-dotted pattern would be maximally useful as protective coloration in the light-dappled environment near the surface. However, records (presumably juveniles) from stomachs of *Alepisaurus* (Fourmanoir 1969) suggest a considerable depth range. A number of juvenile *D. lorum* have been taken from albacore, *Thunnus alalunga*, stomachs, and others have been taken by gear fished near the surface. We see no reason to assume that the albacore had been feeding "far beneath the surface" (Fitch 1964); however, Fitch figured a metamorphosing juvenile of *D. lorum* from an *Alepisaurus* taken on a longline and listed four other such specimens, again indicating a wide depth range. Several of the metamorphosed specimens of *D. lorum* were taken by open nets fished to considerable depths. However, three of the largest specimens were taken in purse seines, indicating depths of capture of no more than 100 m. We have three adult *D. polystictum*: two were taken in nets towed in the upper 500 m, and one was taken in a purse seine.

Fitch's (1964) report on stomach contents provides equivocal evidence; *Idiacanthus* is a mesopelagic vertical migrator, but *Phronima sedentaria* occurs in the upper 300 m (Eric Shulenberger, Scripps Institution of Oceanography, pers. commun.). There is thus no objective evidence that either species of *Desmodema* lives below 500 m (although the possibility is not excluded). The species of *Desmodema* would seem to be members of the deep epipelagic group as defined by Parin (1968).

Keeping in mind the sketchy nature of the available data on depth distribution, the following hypothetical scheme is suggested for both species. The silvery young have a gas bladder. The large fins and the deep head and rapidly tapering body suggest that they are feeble swimmers. They are probably epipelagic. The polka-dotted prejuveniles probably occupy the euphotic zone. The tail is short and anguilliform propulsive waves could involve almost the entire body. The very elongate, fanlike pelvic fins and dorsal pennant indicate that swimming is normally slow and probably involves undulations of the dorsal fin, rather than the body.

With metamorphosis the dorsal pennant and the pelvic fins are lost, the latter dropping off entirely. The tail rapidly elongates at this time (see Figure 5). The polka-dotted pattern is also lost, but more gradually. The greatly elongated tail with its associated dorsal rays would produce drag during active swimming, but probably less so than in *Trachipterus*, in which the posterior part of the body is deeper. We propose that adult *Desmodema* normally occupy the twilight zone of a few hundred meters, where they hover, probably in a head-up posture, maintaining position by undulations of the dorsal fin. Rapid bursts of anguilliform swimming would accompany prey capture or predator avoidance. The tubercle and pore system might act to maintain laminar flow during burst swimming, as hypothesized by Bone (1972) for the oilfish, *Ruvettus*.

The elongate tail of *Desmodema* can be related to the hypothesized mode of life. The lateral line runs the length of the tail, ending at the caudal. The tail then serves the function of greatly extending the lateral line, and in effect provides an an-

tenna for the reception of water displacement and low frequency sound. In this connection it may be pointed out that in the related *Stylephorus chordatus* the lateral line is continued onto the exceedingly elongated caudal filament (R.H. Rosenblatt pers. obs.). *Stylephorus* has tubular eyes directed forward, and it is assumed that it maintains a vertical posture in the water (Marshall 1971:44). That elongate bodies in deep-sea and pelagic fishes are related to a sensory function has been suggested by Wynne-Edwards (1962:80).

Our presumption is that adult *Desmodema* hover vertically, visually seeking prey silhouetted against downwelling light. The lateral-line system of the tail would be used to sense predators approaching beneath the field of view of the eyes. Undulations of dorsal fin would be used for position-holding and the lateral body musculature used for burst swimming for prey capture and predator avoidance.

This mode of life may predominate in the elongate trachipteroids. Nishimura (1963) has inferred a similar life-style for *Trachipterus ishikawai*. Adults of *Zu cristatus* have a long, thin tail, reminiscent of that of the species of *Desmodema*, and Clarke and Haedrich (in Gaul and Clark 1968) recorded the following observation: "A large oarfish, *Regalecus glesne*, was sighted at about 210 meters. It was hanging vertically in the water, head up, and appeared to be almost two meters in length . . . . The dorsal fin was moving continuously with wave-like motions progressing from the head end to the tail end, very much like the fin motions seen in file fish."

Distribution.—Desmodema polystictum is probably circumtropical, and *D. lorum* appears to be restricted to the northern Pacific (Figure 2). The most obvious feature of the distributions is the lack of sympatry. *Desmodema polystictum* is broadly distributed in the tropical Pacific; the northern and southernmost records for the species are in areas influenced by warm currents. *Desmodema lorum* on the other hand is mostly restricted to the cooler waters of the North Pacific. Twenty of the 21 eastern Pacific specimens were taken north of lat. 28°N, that is in areas north of the 20°C August surface isotherm and the 9°C 200-m isotherm. The single western Pacific capture (a metamorphosed juvenile) was in the area where the temperature at 200 m is about 16°C.

The only area of possible sympatry indicated is near Cape San Lucas, lower California, where there are several records of *D. polystictum* and a single record of *D. lorum*. Occurrence of the latter that far south may be related to transport by the California Current.

From Figure 2 it appears that both species of *Desmodema* are especially common in the eastern Pacific. The pattern of captures more likely reflects effort. Many of the specimens of *D. polystictum* have been taken incidentally by the purse seine tuna fishery, which is concentrated in the eastern tropical Pacific. Similarly the predominantly eastern records for *D. lorum* probably reflect the intensive collection effort in the region of the California Current.

The presence of *D. polystictum* in the Atlantic rests on the records of Leapley (1953) and Walters (1963). G. Krefft, Instit für Seefischeri, Hamburg, has informed us that the RV *Walter Herwig* has taken several specimens of *Desmodema* in the central and southern Atlantic, but that the material is not available for study at the present time.

Comparison and relationships.—Walters and Fitch (1960) distinguished *Desmodema* from *Trachipterus* primarily on the basis of the nature of the caudal fin (parallel to the body axis), the length of the gastric caecum (long), the absence of sharp-tipped midventral tubercles, and the presence of scales in *Desmodema*. The last character is not diagnostic, since our study indicates that *D. polystictum* lacks scales at all sizes. The caudal structure of *Desmodema* is unique in the Trachipteridae in that all of the caudal rays are borne on the terminal centrum and the hypural of the first ural centrum is rayless (Figure 1). Additionally, in the species of *Desmodema* there are seven pterygiophores before the first neural spine and one or two between the first and second neural spines, and in *Zu* and *Trachipterus* there is a single pterygiophore before the first neural spine, and nine between the first and second neural spines.

Walters (1963) regarded *Zu* as the most generalized and *Desmodema* as the most specialized of the three trachipterid genera. Despite the specializations unique to *Desmodema* and *Zu* respectively, present evidence indicates that the two genera are more closely related to each other than either is to *Trachipterus*. The most important indicator of relationship if the presence in both of the dermal tubercles in large prejuveniles, and tubercles and a cutaneous pore system in juveniles and adults. Dermal tubercles,

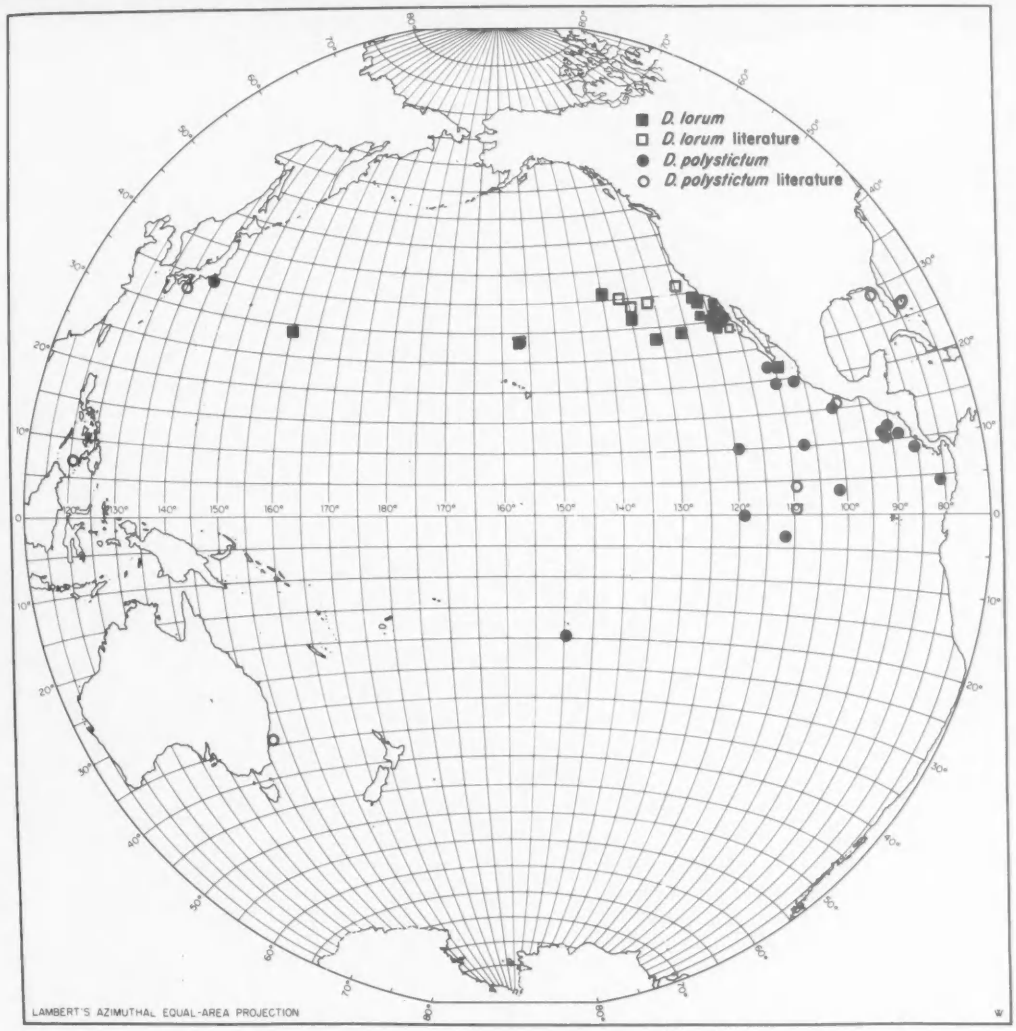

FIGURE 2.—Distribution of the species of *Desmodema*.

pores, and subdermal canals have not previously been reported for *Zu cristatus*. Instead the species has been described as having deciduous cycloid scales (Tortonese 1958; Walters and Fitch 1960; Palmer 1961; Fitch 1964). However, none of our specimens (8, 27.5-811 mm SL) has scales. Two specimens of about 40 mm SL have the skin intact and smooth, except for small tubercles on the lower sides anteriorly, with no trace of scales. Two specimens of 135 and 141 mm SL respectively have the body studded with soft tubercles, with a few interspersed pores; in a specimen of 210 mm SL both tubercles and pores are well developed. In the 811-mm SL adult the skin is superficially very similar to that of *Desmodema*. Our 135-mm SL specimen is from the Atlantic, so it does not appear that we are dealing with a difference between Atlantic and Pacific populations. We can only surmise that the tubercles and pores of *Zu* have been taken to represent scale pockets left behind by

deciduous scales. The "modified cycloid scales" mentioned by Harrisson and Palmer (1968) may have been the dermal tubercles.

In addition to the tubercle and pore system, *Zu* and *Desmodema* agree in two other specialized characters: the body is constricted behind the vent to form an elongated, slender tail, and there is a distinctive prejuvenile which metamorphoses into the juvenile phase.

In our interpretation, *Trachipterus* is the most generalized trachipterid genus, with *Desmodema* and *Zu* specialized in respect to the characters given above. *Desmodema* is advanced with respect to *Zu* in the loss of the lower caudal rays and great elongation of the tail, and probably in the crowding of the pterygiophores before the first neural spine. The significance of the difference in the relationship of the anterior dorsal fin pterygiophores between *Trachipterus* and *Zu* on the one hand and *Desmodema* on the other is difficult to interpret. In *Lophotus* there is a single rayless pterygiophore before the strongly forward-curved first neural spine, then about 15 uncrowded pterygiophores in the wide interspace between the first and second neural spines. The figure of *Regalecus* given by Parker (1886) clearly shows a condition much like that of *Desmodema*. Although the caudal of *Regalecus* has been described as lacking a ventral lobe, we find that two caudal rays are associated with the terminal centrum and four with the (ventral) hypural of the first ural centrum.

Desmodema polystictum (Ogilby)

Figures 3, 4

Trachypterus jacksoniensis polystictus Ogilby 1897:649; Newcastle, New South Wales, Australia; holotype, Australian Museum.

Trachypterus misakiensis Tanaka 1908:52, pl. IV, fig. 2, "shores of Misaki" Japan; holotype, Zool. Inst. University of Tokyo, No. 960. Herre and Herald 1951:318, fig. 3; 6°26′N, 121°35′E.

Trachypterus deltoideus Clark 1938:180; Rurutu Island, "Australs" (Tubuai Islands); holotype, CAS 5532.

Desmodema polysticta. Walters 1963:260; 28°58′N, 88°18′W; Integumentary system. Fitch 1964:230; in part, see synonymy of *D.*

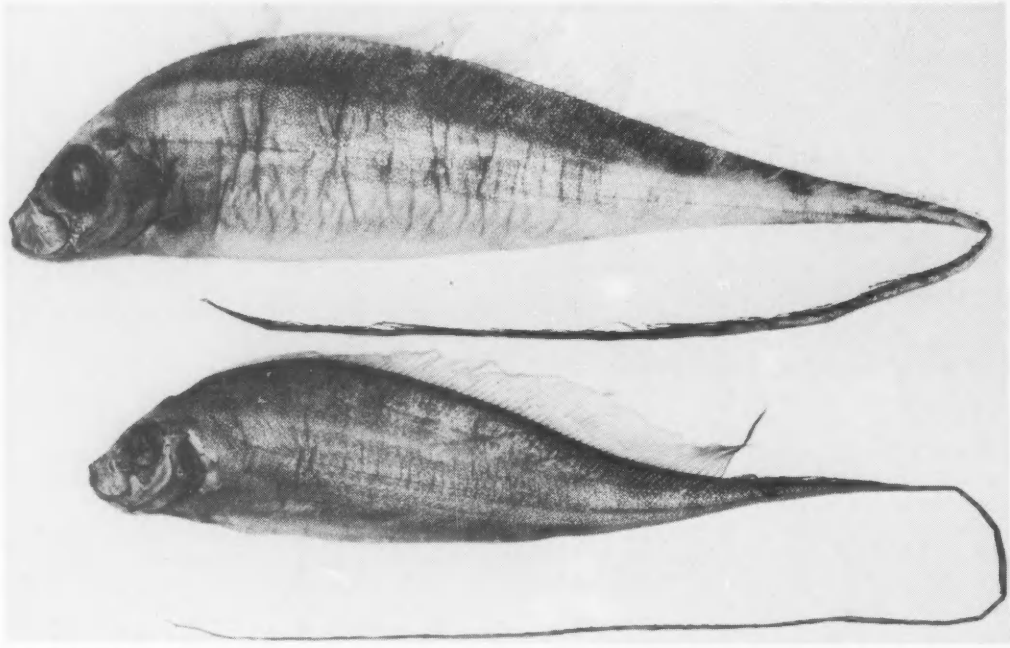

FIGURE 3.—Adults of the species of *Desmodema*. Upper figure *D. polystictum*, SIO 68-333, 1,040 mm SL. Lower figure holotype of *D. lorum*, USNM 216726, 1,098 mm SL.

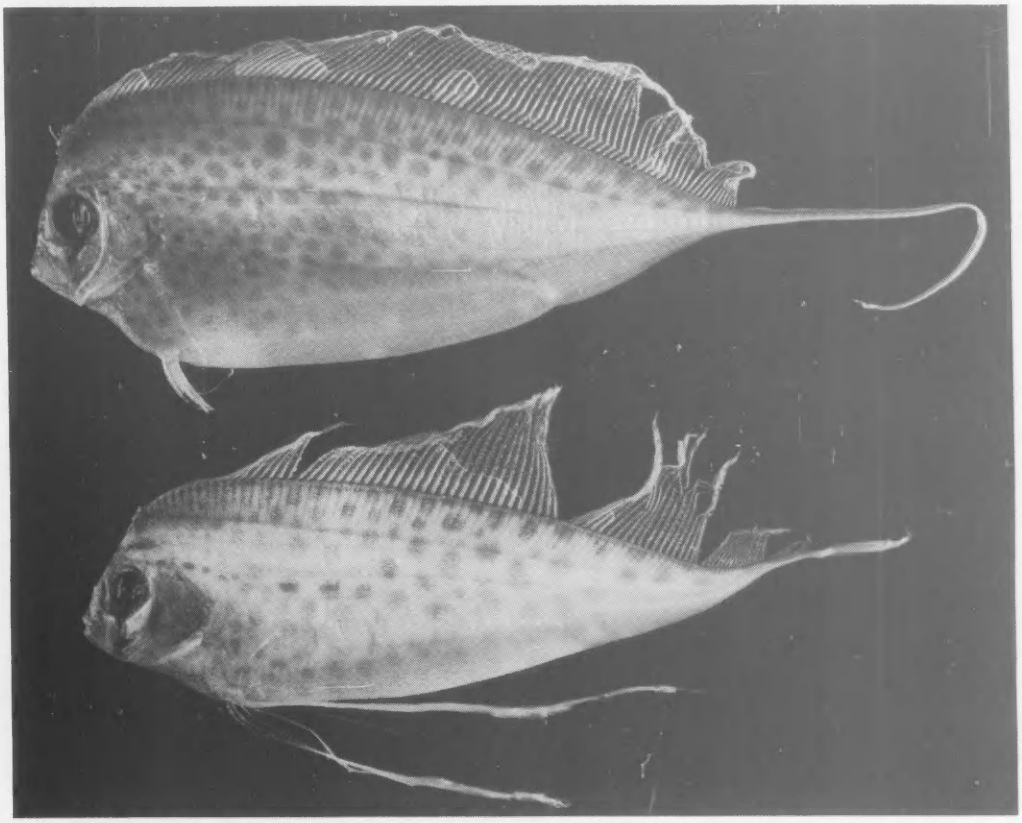

FIGURE 4.—Prejuveniles of *Desmodema*. Upper figure *D. lorum*, LACM 30597-1, 87 mm SV, 188 mm SL. Lower figure *D. polystictum*, SIO 75-55, 85 mm SV, 125 mm SL.

lorum. Fourmanoir 1969:36. Legand et al. 1972:383.

Trachipterus trachyurus, not of Poey. Leapley 1953:236; Fort Lauderdale, Fla.

Diagnosis.—A *Desmodema* with 71-74 total vertebrae (18-20 precaudal and 37-42 before the anus), 7-10 (usually 8) caudal rays, snout length less than eye diameter, attenuate tail in juveniles and adults (Figures 3, 7), and scales absent at all sizes.

Description of adult (see also Tables 1-3).—Ventral profile of body almost straight to anus, then tapering to elongate tail. Dorsal profile rising in a gentle curve to a point a little less than 1 head length behind head, then tapering rapidly to a point about 1½ head lengths behind anus, then tapering more gradually along elongate tail section. Tail long and straplike, postanal length almost two-thirds of standard length. Anus on ventral midline.

Head 2.2-2.5 in snout-vent length, and about 1.3 in greatest body depth. Eye large, diameter slightly greater than snout length. Ascending processes of premaxillae extending back to a point over posterior third of eye.

Dorsal origin over preopercle, preceded by a thickening representing pterygiophores of first six dorsal rays of juveniles. First fin rays short, succeeding rays becoming rapidly longer to about point of maximum body depth, height of fin then increasing more slowly, with longest rays slightly before anus. Behind level of anus fin rays become

TABLE 1.—Regression parameters for selected morphometric characters in *Desmodema*; p = *polystictum*, l = *lorum*.

Characters	Species	Intercept	Slope	Correlation coefficient	*N*
SV vs. SL[1]	p	40.7	0.30	0.97	11
	l	54.8	0.19	0.97	8
HL[2] vs. SV	p	−1.95	0.29	0.95	15
	l	−1.02	0.28	0.98	15
Depth at pelvics vs. SV	p	8.72	0.30	0.97	15
	l	14.57	0.28	0.96	15
Greatest depth vs. SV	p	6.93	0.35	0.97	15
	l	10.66	0.35	0.97	14
Depth at anus vs. SV	p	−0.39	0.20	0.92	15
	l	5.16	0.20	0.97	15
Depth at caudal base vs. HL	p	−0.13	0.02	0.95	11
	l	0.65	0.03	0.78	8
Orbit diameter vs. HL	p	0.05	0.40	0.97	14
	l	0.09	0.36	0.98	15
Eye length vs. HL	p	−0.52	0.38	0.96	14
	l	−0.46	0.33	0.99	14
Snout vs. HL	p	−1.19	0.38	0.99	15
	l	−1.50	0.42	0.93	15
Maxillary length vs. HL	p	0.65	0.37	0.99	15
	l	0.44	0.38	0.99	15
Maxillary width vs. HL	p	−2.27	0.34	0.96	15
	l	−2.81	0.34	0.96	15
Interorbit vs. HL	p	0.31	0.23	0.96	13
	l	−0.56	0.26	0.71	15
Pectoral-pelvic origin vs. HL	p	4.10	0.25	0.97	15
	l	8.07	0.23	0.75	14
Pectoral length vs. HL	p	4.26	0.32	0.95	12
	l	6.69	0.21	0.97	8
Longest dorsal ray vs. HL	p	19.66	0.31	0.81	11
	l	2.90	0.88	0.94	12

[1]SV = Snout vent length, SL = Standard length.
[2]HL = Head length.

TABLE 2.—Caudal and pectoral rays in *Desmodema*.

	Caudal rays							
Species	4	5	6	7	8	9	10	$\bar{x}$
D. polystictum				5	8	1	1	7.9
D. lorum	1	1	9	1				5.8

	Total pectoral rays					
Species	23	24	25	26	27	$\bar{x}$
D. polystictum		5	3	6	2	25.3
D. lorum	2	7	2	3		24.4

rapidly shorter, then fin margin even to caudal base. Pelvics absent but with buried bases still evident. Pectorals low, their bases almost horizontal, outline pointed, tip probably extending almost to lateral line when fin is intact.

Color in alcohol dark brown. Dorsal fin clear, becoming dusky, then black along tail. Caudal black. Pectoral clear. Iris dark, with a golden ring around pupil. In life the fish is silvery with dark red tones dorsally and on the head, and the fins red, except that the dorsal rays along the tail extension are black.

Description of prejuvenile.—Ventral profile of body sloping gradually down from tip of lower jaw to pelvic, then tapering in a gentle curve back to beginning of narrow tail section. Vent asymmetrical, opening on left side. Dorsal profile of head steep, but less so than in *D. lorum* of the same size. In the 44-mm SV individual, the profile is almost vertical to the dorsal origin, but in larger juveniles the slope is gentler, and slightly rounded above the eyes.

Dorsal profile of body curved from dorsal origin to over opercle then tapering back to tail. Point of maximum body depth just behind pelvic bases. Tail extension thin, but relatively short; postanal length about one-quarter of standard length. The narrow part of the tail is characteristically curved upward, so that caudal fin points up and forward.

Head length about 4 in snout-vent length, about 1.6 in greatest body depth. Eye diameter slightly greater than snout length. Ascending processes of premaxillae end over anterior third of eye. Dorsal origin over middle of eye, first five or six dorsal rays elongate, remainder of fin much as in adults.

Pelvic fins present, close together, origin level

TABLE 3.—Vertebral counts in *Desmodema*.

	Precaudal									
Species	18	19	20	21	22	23	24	25		$\bar{x}$
D. polystictum	1	3	3							19.3
D. lorum				2	6	9	2	2		22.8

	Preanal												
Species	37	38	39	40	41	42	. . .	46	47	48	49	50	51	$\bar{x}$
D. polystictum	1	3	1	1	—	1								38.5
D. lorum								3	5	—	5	3	1	48.2

	Total											
Species	71	72	73	74	. . .	106	107	108	109	110		$\bar{x}$
D. polystictum	4	2	—	1								71.7
D. lorum						2	—	2	2	2		108.5

with rear end of pectoral base. Orientation of fin bases and shape of rays as described for *D. lorum*. Pelvics frayed in all specimens, but reaching beyond end of caudal in one and to caudal base in another.

Color in alcohol pale, with a dusky area above and behind head, extending over forehead and anterior to snout tip. Ventral parts of head dusky, a dark streak below eye, running down behind maxilla, a dusky streak along throat to pelvic base. Body with conspicuous black spots which are somewhat larger and more widely spaced posteriorly and above midline. No spots conspicuously larger than others. A narrow dark streak on back along dorsal base, running out to caudal base. Probable life colors, based on two frozen specimens, silver with black spots; iris silver and the dorsal and caudal red; pectorals with pink tinge. This coloration corresponds well with that of the figure given by Tanaka (1908) except that the iris is shown by him as green. Smaller individuals differ (our smallest 32 mm SV) mainly in that the body is less deep and the ventral profile nearly straight, and there are no polka dots. The 37.5-mm SV holotype of *T. deltoideus* was described as "uniform bright silvery." A 55-mm SL individual in poor condition has traces of spots.

Remarks.—Leapley (1953) figured and described a Florida specimen of *D. polystictum* under the name *Trachipterus trachyurus* Poey 1861. The identification was based on the presence of 76 dorsal rays in Leapley's specimen, Poey's specimen having been reported to have 82 dorsal rays.

Leapley's photograph is of a *Desmodema* with a large eye and a relatively deep tail, in agreement with *D. polystictum*. No vertebral counts were given, but Frank Schwartz (pers. commun.) has supplied vertebral counts for Leapley's specimens, as well as an additional individual from the western North Atlantic. Both have 18 precaudal vertebrae, also in agreement with *D. polystictum*.

If Leapley's identification were correct, Poey's name would be a senior synonym of *Desmodema polystictum* (Ogilby 1897). However, three characters indicate that *D. polystictum* cannot be identified with *T. trachyurus*. These are number of ventral rays (6 in *trachyurus*, 8 or 9 in *polystictum*), pectoral rays (15, vs. 12-14), and coloration (silvery with a midlateral yellow band vs. polka-dotted). In addition, *T. trachyurus* was described as having vertebral processes piercing the skin (probably an artifact caused by postmortem drying) and lacking elongated anterior dorsal rays (present in all juvenile trachipterids).

The supposed agreement in low number of dorsal rays is invalid, since Leapley's specimen was broken far in advance of the caudal. Using his value for body depth of his specimen (141 mm) we estimate the actual length to have been between 1,400 and 1,500 mm. Poey's description does not allow the identification of *T. trachyurus* with any known trachipterid. *Zu cristatus* is excluded because juveniles of that form are strongly barred and have peculiar fleshy abdominal lobes that are unlikely to go unmentioned in a description.

The species of *Trachipterus* are not completely understood, but juveniles of that genus have dark markings, a dorsal pennant, and tubercles along the venter.

Material examined.—Western and Central Pacific: CAS SU 23783, Sagami Bay 1(72.8, 102.5); CAS 5532, Rurutu, Tubuai Islands 1(37.5, 49.9), holotype of *Trachipterus deltiodeus*. Eastern Pacific: UCLA W58-103, 96 km southwest of Cabo San Lucas, Baja California, tuna purse seine, 2(66, 91 and 88, 125); SIO 70-142, 19°50′N, 106°15′W, tuna purse seine, 1(260); SIO 68-33, 19°53′N, 110°46′W, "5 × 5" nekton net towed at 5 knots, 800 m wire out, 1(333, 1,040); SIO 63-915, 16°01.5′N, 100°54′W, "5 × 5" nekton net, 0-200 m, 1(277, 785); SIO 76-167, 12°55′N, 90°54′W, tuna purse seine, 1(111.5); SIO 76-294, 12°35′N, 92°15′W, tuna purse seine, 1(84.9, 126.5); SIO 76-67, 12°15′N, 92°25′W, tuna purse seine, 1(42); UCLA W67-135, 11°48′N, 88°25′W, 1(60 SL); SIO 73-392, 11°18′N, 91°31′W, tuna purse seine, 1(91.5); SIO 75-139, 10°00′N, 119°00′W, midwater trawl, 0-50 m, 2(74.3, 100.5 and 90 SL); SIO 76-325, 10°24′N, 107°46′W, midwater trawl, 225 m wire out, 1(25.5); SIO 73-400, 08°41′N, 85°03′W, dipnetted at surface, 1(82); SIO 64-397, 03°18.4′N, 101°54.3′W, stomach of *Alepisaurus ferox* 1(55.5); SIO 63-299, 04°03′N, 80°46′W, meter net, 400 m wire out, 1(23); SIO 75-590, 00°00.2′S, 119°17.0′W, meter net, 0-200 m, 1(28.0, 36.0); SIO 52-334, 02°47′S, 112°13′W, meter net, 0-250 m, 1(29, 40.5); SIO 73-340 "Eastern N. Pacific," tuna purse seine, 1(296, 835).

Desmodema lorum n.sp.

Figures 3, 4, 5, 6

Desmodema polysticta, not of Ogilby. Fitch

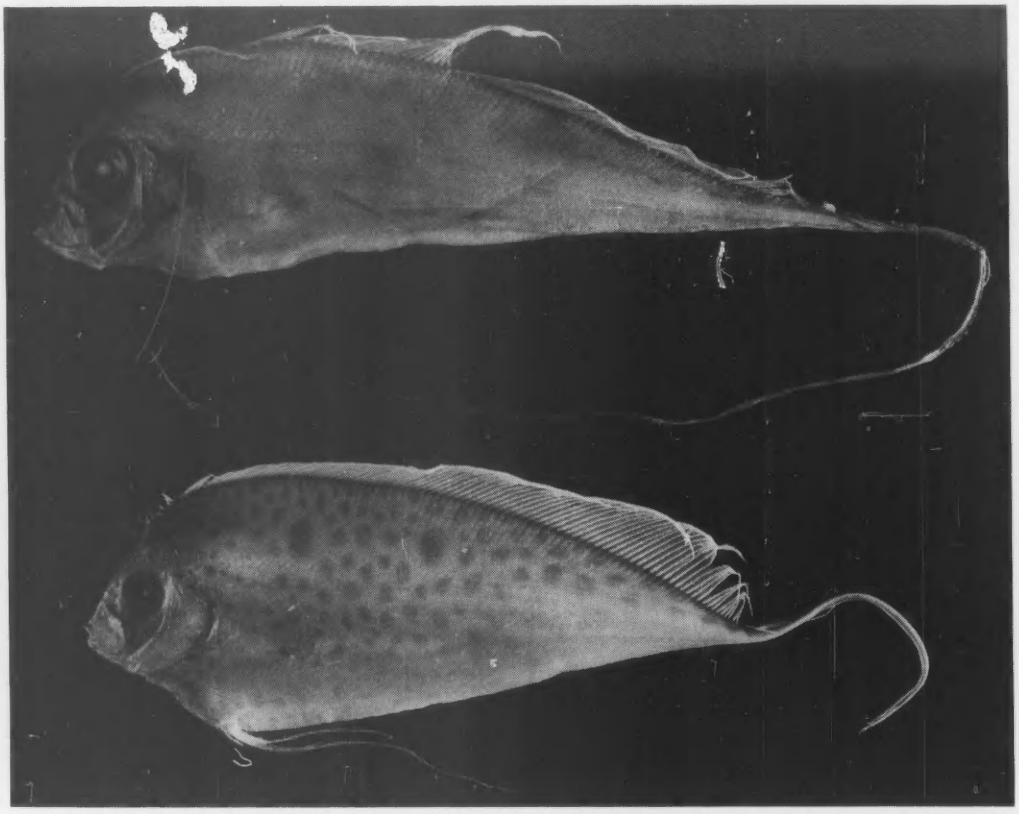

FIGURE 5.—Juvenile and prejuvenile of *Desmodema lorum*. Upper figure juvenile, LACM 35237-1, 103.7 SV, 412 mm SL. Lower figure prejuvenile, LACM 30230-l, 95 mm SV, 198 mm SL.

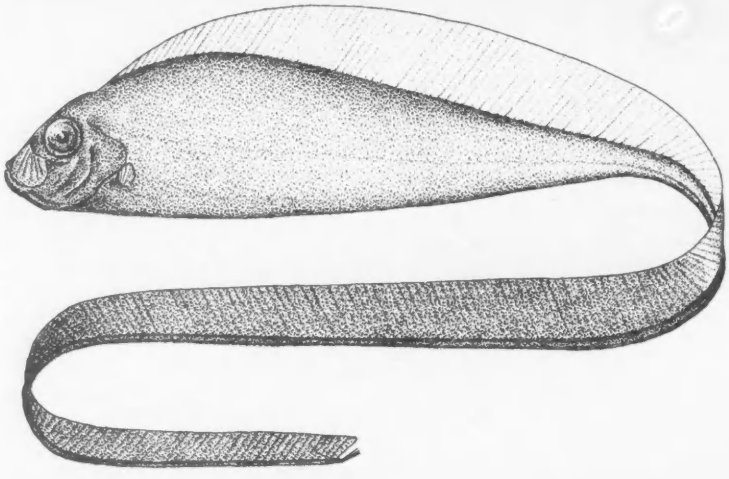

FIGURE 6.—Holotype of *Desmodema lorum*, USNM 216726. Fins reconstructed.

1964:321; in part, all but 10th, 12th, 13th of listed specimens (fig. 2 is *D. lorum*, fig. 3 is *D. polystictum*).

Desmodema polystictum, not of Ogilby. Berry and Perkins 1966:668. Fitch and Lavenberg 1968:88. Miller and Lea 1972:87.

Desmodema polystictus, not of Ogilby. Radovich 1961:18.

Diagnosis.—A *Desmodema* with 106-111 total vertebrae (21-25 precaudal and 46-50 before the anus), 4-7 (usually 6) caudal rays, snout length greater than eye diameter, an exceedingly long attenuate tail in juveniles and adults (Figures 3, 7) and scales present in prejuveniles and small juveniles.

Description of adult (see also Tables 1-3).—Ventral profile of body almost straight, but with a slight convexity back to anus, then tapering back to elongate tail section. Dorsal profile rising rapidly from snout tip to dorsal origin, then ascending more gently to maximum depth of body about one-half to three-quarters of head length behind head, then tapering back to tail. Tail exceedingly long and narrow, postanal length three-quarters of standard length. Anus on ventral midline.

Head length 3.2-3.8 in snout-vent length, 1.2-1.3 in greatest body depth. Eye moderate, equal to or (usually) shorter than snout. Ascending processes of premaxillae ending over or behind rear margin of eye. Dorsal origin just behind preopercle to over middle of opercle, preceded by a horny process representing pterygiophores of first six dorsal rays. First few dorsal rays short, succeeding rays becoming longer, with maximum height of fin over and posterior to anus. Fin height decreases gradually along tail, probably as reconstructed in Figure 6. Pelvics absent, but with buried bases still evident. Pectorals low, their bases horizontal. Pectoral pointed, but tip frayed and broken in all specimens.

Color in alcohol tan. Dorsal fin clear, becoming dusky, then black along tail. Caudal black. Pectorals clear. Iris dark with a golden ring around pupil. In life, probably silvery with red tones dorsally and on the head, and with the fins red.

Description of prejuvenile.—Ventral profile sloping down from tip of lower jaw to pelvics, then tapering convexly back to vent, then tapering more sharply to beginning of tail, then straight.

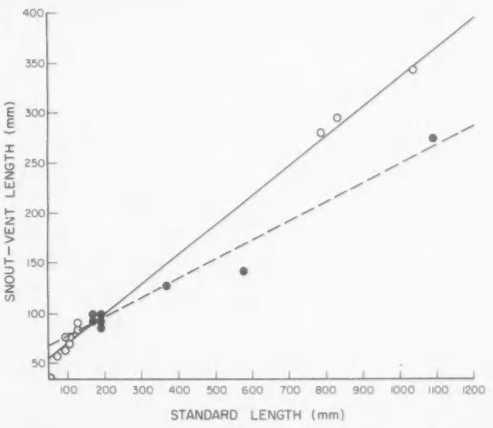

FIGURE 7.—The regression of snout-vent length on standard length in *Desmodema*. Open circles *D. polystictum*, closed circles *D. lorum*.

Usually a notch in outline at position of vent, which is asymmetrical, opening on the left side. Dorsal profile of head steep, almost vertical in smaller specimens. Back curved, point of maximum body depth just behind pelvic base. Dorsal profile becomes straight along tail elongation. Tail long and thin, postanal length about one-half of standard length.

Head length 3.8-4.2 in snout-vent length, 1.8-2.2 in greatest body depth. Eye about equal to snout length. Because of the steepness of the forehead, the ascending processes of the premaxillae end over the anterior third of the eye.

Dorsal origin over middle to posterior third of eye. First five or six dorsal rays elongate, remainder of fin shaped much as in adult except that the rays along the elongate tail are not as long. Pelvic fins present, close together, origin under pectoral base. Anteroposterior axes of pelvics parallel with sides. Pelvics broken in all our material, but reaching beyond anus in one specimen. Pelvic rays flattened and bladelike basally, the first the broadest, becoming filamentous distally. Minute prickles along rays. Pectorals as in adults.

Color in alcohol tan, a darker area on back over and behind head, extending down over forehead onto snout. A variably developed dusky streak from lower margin of orbit down behind maxilla. A dusky streak along throat to pelvic bases. Spotting somewhat variable but spots becoming larger and more widely spaced posteriorly and above midline. Three of five specimens with two noticeably larger

spots on upper back on middle-third of body (see Figure 4). A narrow dark streak on back at base of dorsal, broadening on narrow part of tail. Individuals of about 35 mm SV differ in that the body is not so deep, and there is little or no pigment. Also the dorsal is relatively higher. Our smallest specimen, 18.5 mm SV, has the back with a straight taper behind the head, the ventral profile more evenly tapering, and has scattered melanophores on the head and over the viscera. These probably represent the larval pigmentation.

Identification and remarks.—The characters given in the generic and specific diagnoses serve to distinguish *D. lorum* adequately from all known trachipterids. In addition to the characters given in the diagnoses, the two species of *Desmodema* differ in number of dorsal rays. The single *D. lorum* counted had 197 dorsal rays and three *D. polystictum* had 120, 124, and 121, respectively. Another feature is the height of the dorsal. Large *D. lorum* have proportionately longer dorsal rays than do *D. polystictum* of equivalent size (Figure 8, Table 1). Prejuveniles of *D. lorum* can most easily be distinguished from those of *D. polystictum* by their deeper body, and more rounded anteroventral contour (Figure 4).

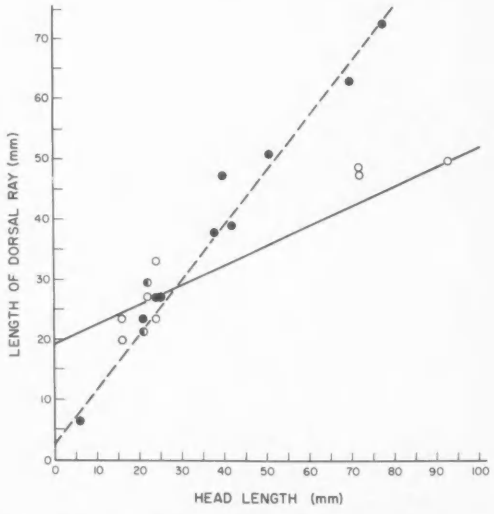

FIGURE 8.—The regression of length of longest dorsal ray on head length in *Desmodema*. Open circles *D. polystictum*, closed circles *D. lorum*.

Although Ogilby did not illustrate the holotype of *Trachypterus jacksoniensis polystictus*, his description is sufficiently detailed to allow identification with considerable certainty. The polka-dotted coloration and lack of lower caudal lobe are diagnostic of *Desmodema*, and the dorsal ray count of 126 indicates that our material has been correctly assigned. The caudal count of seven or eight rays also accords with our concept of *D. polystictum*. Tanaka's (1908) excellent figure indicates that *Trachypterus misakiensis* has properly been synonymized with *D. polystictum*, and the presence of eight caudal rays in the small holotype of *Trachipterus deltoideus* dictates a similar placement.

Etymology.—From the Latin *lorum*, a whip, in reference to the elongate tail. Suggested common name, whiptail ribbonfish.

Material examined.—Holotype: USNM 216726, formerly SIO 62-434, a 1,098 mm SL (276 mm SV) male, taken between 29°05′N, 126°37′W and 29°03′N, 126°42′W by RV *John N. Cobb* with a Cobb Mk II trawl with 1,200 m wire out (estimated fishing depth 400 m) between 1930 and 2110 h on 25 August 1962. (Original station number 90.160, C6208, see Berry and Perkins 1966.) Paratypes: LACM 30217-1, 34°42′N, 121°20′W, spit up by *Thunnus alalunga*, 1(91.5, 167); LACM 9890-2, 34°25′N, 120°28′W, 15.2-m midwater trawl, 8 fm, 1(97, 173); LACM 9982, 33°00′N, 118°03′W, IKMT, 2,743 m wire out, 1(131); SIO 76-335, 13 km west of Oceanside, Calif., bait net, 1(95, 198); LACM 30597-1, 32°48′N, 118°16′W to 32°30′N, 118°30′W, IKMT, 1(87, 188); LACM 35237-1, 32°43′N, 118°57.5′W, 10-m midwater trawl, 1(103.7, 412); LACM 31678-1, San Clemente Island, Calif., off Pyramid Head, 1(83); LACM 30998-1, 31°45′N, 118°48′W to 31°44′N, 118°00′W, IKMT, 1,300 m, 1(93); SIO 63-375, 31°40.5′N, 122°03.5′W to 31°37.0′N, 122°04.3′W, Cobb Mk II trawl, 1,144 m wire out, 1(139.8, 580); SIO 63-429, 29°58.5′N, 120°07′W, IKMT, 4,500 m wire out, 1(173); LACM 9726-8, 29°29′N, 118°35′W, IKMT, 2,134 m wire out, 1(92.5, 189); SIO 74-47, 28°10.2′N, 160°00.9′E, IKMT, 0-1,000 m, 1(125, 364); UCLA W61-125, 64 km off Cabo Colnett, Baja California, 1(286), LACM 31800-2, 129 km south of Cabo San Lucas, Baja California, 1(283).

Additional material.—UCLA W55-320,

33°39′N, 135°00′W, 1; SIO 75-588, 29°17′N, 116°59′W, 1(55); UCLA A343, 28°N, 132°W, 1; UCLA W62-73, 32°10′N, 118°24′W, 1(53); SIO 75-589, 28°37.5′N, 118°18′W, 1(18.5); SIO 75-591, 33°34′N, 118°34′W, 1(89+ SL); LACM 31804, no data, 1(132); SIO 64-96, 31°39′N, 117°51′W, 1(289); SIO 72-16, 27°22′N, 155°23′W, 1(19.8, 26.4).

ACKNOWLEDGMENTS

We thank William Eschmeyer (CAS), Robert Lavenberg (LACM), and Boyd W. Walker (UCLA) for permission to examine specimens under their care. Gary L. Friedricksen turned three specimens over to us. John Fitch supplied collection data for certain specimens and read the manuscript. Robert Lavenberg and John Fitch supplied the original of the drawing of the holotype of *D. lorum*, first published in Fitch and Lavenberg 1968. Frank Schwartz, Institute of Marine Science, University of North Carolina, supplied vertebral counts of two Atlantic specimens of *D. polystictum*.

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OXYCLINE CHARACTERISTICS AND SKIPJACK TUNA DISTRIBUTION IN THE SOUTHEASTERN TROPICAL ATLANTIC

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ABSTRACT

A shallow layer of low oxygen concentration, containing minimum values frequently less than 1.0 ml/l and a strong oxycline, was measured on two cooperative cruises in the southeastern tropical Atlantic Ocean and found to be consistent with previous portrayals and hypotheses based on fragmentary data. The low-oxygen layer was in the form of a thick wedge off the southwestern coast of Africa, extending from about lat. 18° to 3° S. The oxycline overlying the low-oxygen layer was generally coincident with a pycnocline and was found at depths of 20-50 m in most of the area surveyed, as revealed by the topography of the 3.5 ml/l iso-oxygen surface. It is believed that a shallow oxycline has a strong influence on the distribution and availability of skipjack tuna schools. The hypothesis was tested by overlaying school sighting positions on the 3.5 ml/l topography. The association between sightings and oxycline depth was further defined by developing a linear "equation" relating the two variables as follows: $s = 23.15 - 0.59z$, where s is the number of school sightings, z is the depth of the 3.5 ml/l surface, and 23.15 and 0.59 are constants. A similar correlation was attempted with school sightings and habitat layer thickness, but the results were less systematic and convincing than the oxycline correlation.

A shallow oxycline containing low values of dissolved oxygen concentration should serve as a lower boundary of the environment habitable by surface schooling tunas. In a study of the relationship of thermocline depth to success of purse seining of tuna in the tropical Pacific, Green (1967) stated that an oxycline approximately coincident with the thermocline could play a major role in restricting the fish to near surface waters. Work on the oxygen requirements of captive skipjack tuna in the Southwest Fisheries Center Honolulu Laboratory[3] by R. M. Gooding and W. H. Neill indicated a 4-h TL_m (median tolerance limit) between 2.4 and 2.8 ml O_2/l, and in experiments with gradually declining oxygen concentrations an alarm threshold was found near 3.5 ml/l. If we regard the 3.5 ml/l iso-oxygen surface to be the "floor" of habitable environment of surface schooling tunas in tropical waters, then the topography of this surface becomes significant in describing their environment.

The shoaling of the oxycline, the floor of the habitable environment, may serve not only to crowd the skipjack tuna schools to the surface, but also to influence the lateral distribution of the fish schools through other ecological factors associated with the shoaling. The oxycline is imbedded in the thermocline, which is brought up to or near the sea surface under conditions of upwelling which seasonally occur off the southwestern coast of Africa. Such conditions, when well developed, will lead to the development of fronts, which tend to concentrate forage, and higher rates of primary and secondary productivity to sustain larger forage populations; both processes tending to concentrate predators such as tunas, as described by Blackburn (1965).

BACKGROUND INFORMATION ON OXYGEN MINIMA IN THE SOUTHEASTERN ATLANTIC

The oxygen minima in the Atlantic have been studied since the early part of this century. These studies have not, however, resulted in a definitive explanation of the mechanisms of formation of these low-oxygen layers. While many theories have been proposed to explain the origin of these layers, the mechanisms generally cited as being most significant are either an extremely high biochemical oxygen consumption or low rates of oxygen replenishment by mixing processes. Some recent papers have dealt with a synthesis of these

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[3]Neill, W. H. Unpubl. exp. data, Southwest Fish. Cen. Honolulu Lab., Natl Mar. Fish, Serv., NOAA, pers commun., 1974 and 1976.

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processes in an attempt to give a more complete explanation of the observed patterns (Wyrtki 1962; Bubnov 1966, 1972; Menzel and Ryther 1968).

Proponents of the first mechanism argue that an oxygen minimum layer is formed as a result of biochemical oxidation of organic matter that has accumulated at intermediate depths due to specific gravity relationships between seawater and sinking detritus (Seiwell 1937; Miyake and Saruhashi 1956). Those supporting the second mechanism suggest that an oxygen minimum will be formed at the relatively still boundary between circulating water masses where replenishment of oxygen will be minimal. This view was first advanced by Jacobsen in 1916 and was later supported by Dietrich and Wüst (Richards 1957).

More recent studies (Redfield 1942; Wyrtki 1962; Bubnov 1966, 1972; Menzel and Ryther 1968) have stressed the importance of advective processes in the formation of oxygen minimum surfaces. Redfield (1942) hypothesized that the deep oxygen minimum of the Atlantic could be formed by advection along isentropic surfaces of water carrying a heavy load of organic detritus and solutes from high latitude convergence areas. Subsequent oxidation of the organic load forms a minimum. Wyrtki (1962), Menzel and Ryther (1968), and Bubnov (1966, 1972) considered high oxygen consumption as necessary for initial formation of low-oxygen water with advective and mixing processes controlling its position and movement. Wyrtki (1962) contended that oxidation occurring in the layer of least advection results in formation of an oxygen minimum, which can spread by mixing into other water masses. Menzel and Ryther (1968) and Bubnov (1966, 1972) argued that oxygen depleted water will form in specific areas due to high biochemical oxygen consumption and that these waters are then spread by advection and turbulent diffusion.

Bubnov (1972) stated that the main factors controlling the formation of an oxygen minimum are the rate of biochemical oxidation, the density stratification of the water, and the supply of oxygenated water to bottom layers. In the southeastern tropical Atlantic the presence of one or more of these factors results in highly favorable conditions for the formation of an oxygen minimum. The coastal region off South-West Africa has strong upwelling conditions which result in high organic production and subsequent high oxygen consumption (Hart and Currie 1960). Though the coastal waters are weakly stratified in comparison with the region of the Congo River effluent, there is, nonetheless, a well-developed pycnocline which inhibits downward-mixing of highly oxygenated surface waters (Visser 1970; Bubnov 1972). In addition, the deep waters of the Angola Basin are somewhat lower in oxygen than those of the western basin of the South Atlantic. This reduces the amount of oxygen which will be mixed into the upper layers by upwelling or turbulent diffusion (Bubnov 1972). Taft (1963) and Visser (1970) suggested that the waters to the north of lat. 20°S off the coast of South-West Africa may be isolated from the highly oxygenated deepwater masses formed at high latitudes, thus inhibiting the renewal of oxygen from this source.

Because of the favorable conditions for the formation of low-oxygen water in the coastal region of South-West Africa, it has been suggested that this area is a source for much of the water that forms the oxygen minimum surfaces in the South Atlantic. Taft (1963) plotted the oxygen and salinity distributions on surfaces of constant potential specific volume anomaly for the South Atlantic. On the 125, 100, and 80 cl/t surfaces (σ_θ 26.81, 27.07, and 27.49 g/l, respectively), the isopleths of both oxygen and salinity are zonal at lat. 20°S. The areas of lowest oxygen concentration are located just north of lat. 20°S off the coast of South-West Africa, strongly suggesting that this region serves as a source area for low-oxygen water which is then transported westward to form the primary minimum at 300-600 m in the study area).

In a study by Menzel and Ryther (1968), the concentration of dissolved organic carbon in the South Atlantic was found to be essentially constant below 400-500 m while the oxygen content varied. Based on this finding, they concluded that oxygen concentrations in the minimum layer will not be further reduced by in situ decomposition of organic matter. They suggest that low-oxygen water is formed off South-West Africa and is then distributed horizontally along isentropic surfaces to form the primary oxygen minimum layer. Changes in the oxygen content occur by mixing with water masses of higher oxygen content, resulting in the increase of oxygen concentrations as the water moves farther from its source.

Bubnov (1972) identified three areas off South-West Africa where waters of very low oxygen content are formed (see Figure 1): 1) the shelf region to the south of lat. 17°S, 2) the coastal

region extending from long. 8°-10°E to the shelf, and from lat. 7°-9°S to 17°-18°S, and 3) the region of the quasi-stationary cyclonic gyre to the west of long. 6°E.

In the shelf region south of lat. 17°S, water with extremely low-oxygen content (<1 ml/l) forms in the near-bottom layer (80-150 m) and spreads northward and westward beneath the warmer, less dense surface water by advection and turbulent diffusion. This water forms the shallow minimum layer that is characteristic of this region, extending westward to about long. 0° where it loses its identity due to mixing.

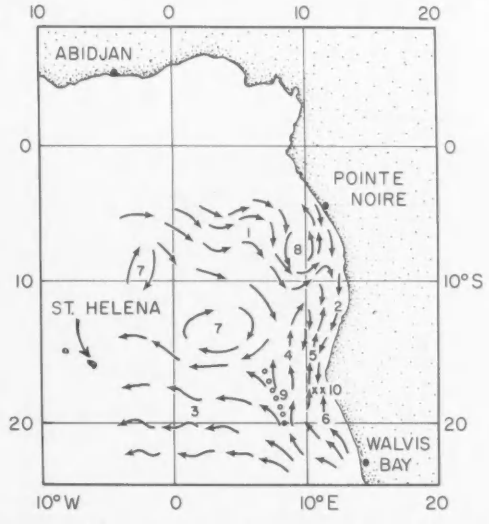

FIGURE 1.—Diagram of geostrophic water circulation in the 0 to 100 m layer. 1) South equatorial countercurrent; 2) Angola Current; 3) west (main) branch of Benguela Current; 4, 5, 6) north branches of Benguela Current; 7) eddies in inner region of cyclonic gyre; 8) anticyclonic curl; 9) Benguela divergence; 10) merging zone of Angola Current and north littoral branch of Benguela Current. From Moroshkin et al. (1970).

The "eastern coastal region" and the region of the cyclonic gyre are areas where low-oxygen water (<1 ml/l) forms at "intermediate" depths (Bubnov 1972). These waters apparently are advected and mixed to the west, forming the primary oxygen minimum in the eastern South Atlantic. These observations provide further evidence to support the hypothesis that the coastal waters off Southwestern Africa are a source for much of the low-oxygen water that forms the oxygen minima in the South Atlantic.

RESULTS OF JISETA CRUISES

In 1968 the National Marine Fisheries Service, then Bureau of Commercial Fisheries, joined with the U.S. Coast Guard and the Missao de Estudos Bioceanologicos e de Pescas de Angola in the Joint Investigation of the Southeastern Tropical Atlantic (JISETA); an oceanographic and biological investigation in the coastal waters of southwestern Africa. Distribution of tunas and oceanographic conditions from the Equator to lat. 18°S were investigated on cooperative cruises of the RV *Undaunted*, the USCGC *Rockaway*, and the RV *Goa* during February through April and September through December 1968.

Low-Oxygen Layer

Vertical sections of dissolved oxygen concentration developed from the JISETA data (Cook et al. 1974) characteristically showed a layer of low oxygen concentration, including a minimum which frequently was <1.0 ml/l and occasionally <0.5 ml/l in concentration. The minimum values were not well defined because of the means of sampling employed: 1 cast of 10 Niskin bottles spaced throughout the upper 1,000 m of the water column at each station. However, the samples were spaced well enough to portray the layer of low concentration and the sharp oxycline which formed its upper boundary.

The transects obtained in March 1968 (Figures 2, 3) showed a layer of oxygen concentration <1.0 ml/l of variable thickness (50-450 m) extending from lat. 15° to 18°S in the upper 500 m of the water column. In the southern portion of the area the layer was thicker and nearer the sea surface.

In the October-November transects (Figures 4, 5) a thick layer of water containing <1.0 ml/l dissolved oxygen was found to extend from lat. 17° to 7°S in the upper 600 m of the water column. Once again the layer was thicker (up to 550 m) and nearer the surface in the southern portion of the area. In the northern portion it thinned to <100 m and was detected at about 300-400 m depth at the outer stations, about n.mi. (180 km) offshore.

The form of the layer of very low oxygen concentration (<1.0 ml/l) observed in October-November 1968 (Figure 6) appears to be consistent with Bubnov's (1972) contention that the source of the layer is located in coastal waters between lat. 18° and 23°S, from which it is advected northward by the northern branches of the Benguela Cur-

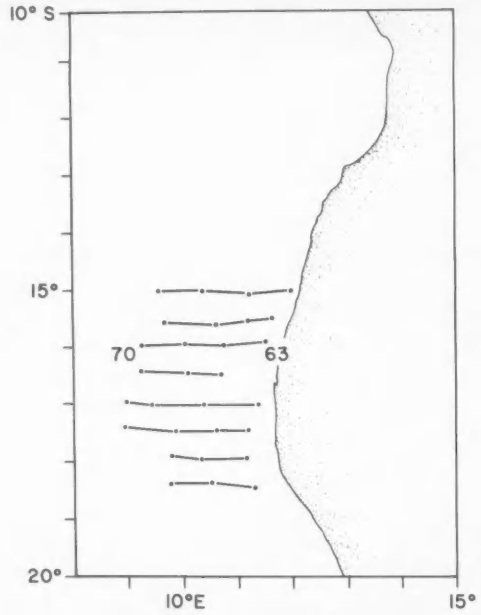

FIGURE 2.—Locations of transects of dissolved oxygen concentration conducted by *Undaunted* during 8-16 March 1968. From Cook et al. 1974.

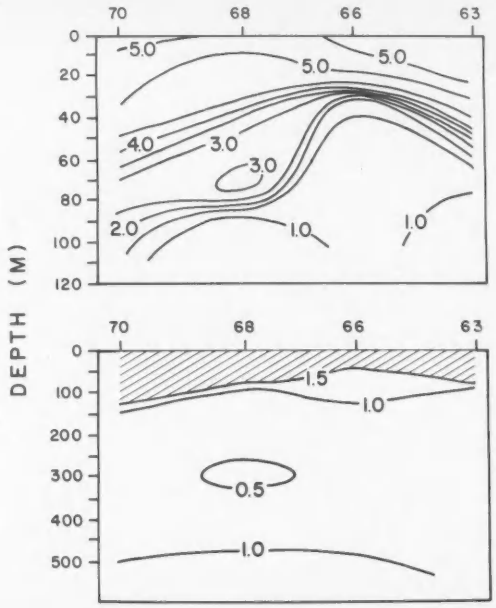

FIGURE 3.—One of the transects of dissolved oxygen concentration (milliliters per liter) produced from *Undaunted* data (8-16 March 1968). From Cook et al. 1974.

rent. The apparent divergence of the layer from the coast shown in the onshore-offshore transects north of lat. 9°S (Cook et al. 1974) also is consistent with the general direction of flow given for the extension of the current.

Although a subsurface oxygen minimum was found throughout the area surveyed from lat. 18°S to the Equator, the layer of very low oxygen concentrations (≤1.0 ml/l) extended northward only as far as lat. 7°-8°S. The increase in oxygen concentration northward from those latitudes is the result of either westward turning of the northward current as carrying the low oxygen concentrations as suggested by Bubnov (1972) or increased mixing rates attenuating the oxygen minimum.

Oxycline

Overlying the layer of low oxygen concentration throughout its extent was an intense oxycline. The range of concentrations in the oxycline usually was from 2.0 to 4.0 ml/l, but was found to be as great as from 1.0 to 5.0 ml/l in the southern portion of the surveyed area. The oxycline thickness ranged from about 40 m to 10 m, producing intense vertical gradients when thinnest. The most intense gradients were found on the shoreward ends of the transects and in the southern portion of the surveyed area.

The 3.5 ml/l iso-surface was selected to portray oxycline topography because it was found in the upper oxycline throughout the area surveyed (lat. 18°S-Equator) and because this oxygen concentration has been found to be significant in the physiology and distribution of skipjack tuna in the eastern tropical Pacific (Neill see footnote 3; Barkley et al.[4]). The resulting topographies for the February-April and October-November periods (Figures 7, 8) were generally of low relief and shallow (≤50 m) except at the seaward end of transects south of lat. 16° S in March and north of lat. 2°-3° S in October-November. Two large areas of shallow depths (≤25 m) to the oxycline were found in the October-November data field, from lat. 10° to 16°S and from lat. 5° to 7°S. Due to the

[4]Barkley, R. A., W. H. Neill, and R. M. Gooding. 1977. Skipjack tuna habitat based on temperature and oxygen requirements. Unpubl. Manuscr. 12 p. Southwest Fish. Cen. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

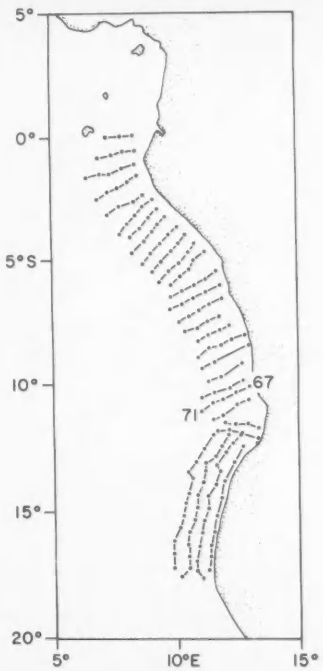

FIGURE 4.—Location of transects of dissolved oxygen concentration by *Undaunted* and *Rockaway* 15 October-21 November 1968. Derived from Cook et al. 1974.

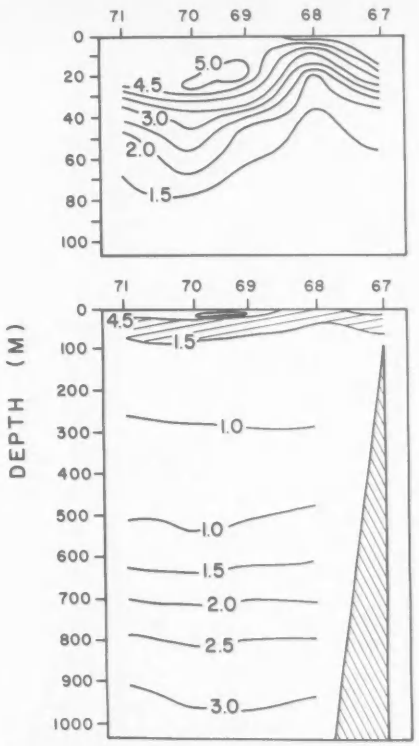

FIGURE 5.—One of the transects of dissolved oxygen concentration (milliliter per liter) produced from *Undaunted* data (22-23 October 1968). From Cook et al. 1974.

relatively incomplete sampling grid in the February-April period, little can be learned from any attempts to compare the results of the two periods.

Pycnocline

The density field of the upper waters off southwestern Africa is determined mostly by temperature, except in the area influenced by the effluent of the Congo River (Bubnov 1972). Results of the JISETA cruises support this contention, showing a well-developed thermocline throughout the area.

During the October-November period thermocline gradients increased from south to north with the most intense gradients found off the Congo River. The sea-surface temperature ranged from <17° C in the south (lat. 18° S) to >26° C near the Equator. In the February-April period the thermocline appeared to be more intense than during the October-November period but generally con-

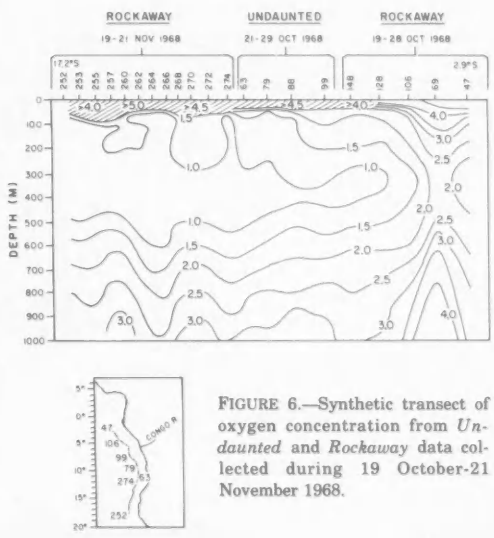

FIGURE 6.—Synthetic transect of oxygen concentration from *Undaunted* and *Rockaway* data collected during 19 October-21 November 1968.

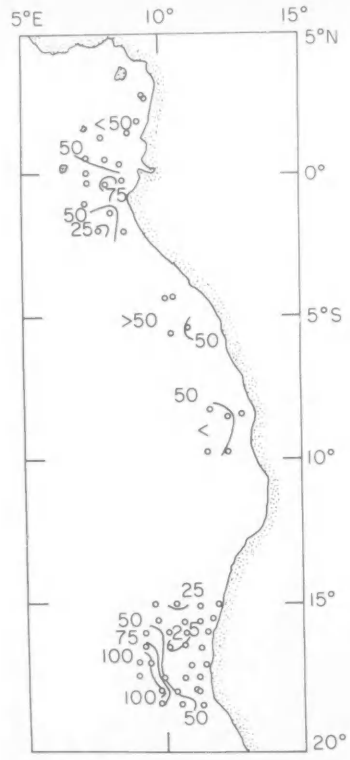

FIGURE 7.—Depth (meters) to the 3.5 ml/l iso-oxygen surface from *Undaunted* data, February-March 1968.

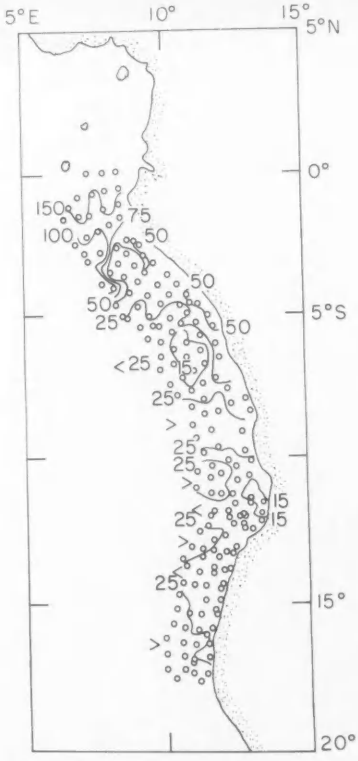

FIGURE 8.—Depth (meters) to the 3.5 ml/l iso-oxygen surface from *Undaunted* and *Rockaway* data, October-November 1968.

stant throughout the limited area surveyed. The sea-surface temperature ranged from 22°C in the south (lat. 18°S) to 29°C in the north (lat. 2°N).

In order to portray the pycnocline topography and minimize the differences in surface heating in the two periods, an isopycnal surface found near the bottom of the thermocline, the $\sigma_t = 26.0$ surface, was chosen (Figures 9, 10). Comparison of the vertical sections of density and oxygen from the JISETA cruises (Cook et al. 1974) shows that the 26.0 iso-σ_t surface parallels the oxycline and is found in its lower levels. Therefore the topography of the isopycnal surface also should reflect geostrophic circulation patterns in the lower oxycline.

During the October-November 1968 period the 26.0 g/l topography (Figure 10) deepened nearshore north of lat. 10°S, but was shallow and irregular south of there. The topography north of lat. 10°S indicates a general southward flow in the upper layer from about lat. 4° to 10°S, corresponding with the southward Angola Current described by Moroshkin et al. (1970), but not extending as far south as they portray it (Figure 1).

RELATIONSHIP BETWEEN OXYCLINE DEPTH AND SKIPJACK DISTRIBUTION

Variations in the thickness of the habitable environment of skipjack tuna, bounded beneath by the oxycline, should strongly inflence the distribution and availability of surface schooling tunas. To test this contention, the positions of sightings of skipjack schools during the October-November 1968 cruise period were plotted on a map of oxycline (3.5 ml/l) topography (Figure 11). A cursory study of this plot reveals that the fish were generally sighted where the oxycline was <50 m deep, and over 80% of the schools were seen where it was <30 m deep.

An apparent relationship between school distribution or availability and oxycline depth can

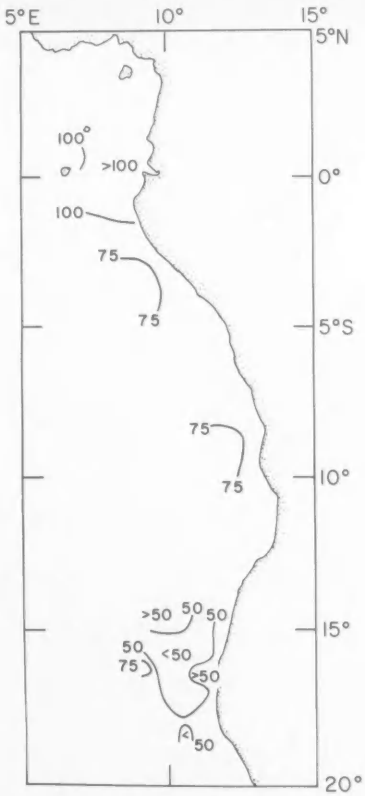

FIGURE 9.—Depth (meters) to the 26.0 g/l σ_t surface from *Undaunted* data, February-April 1968.

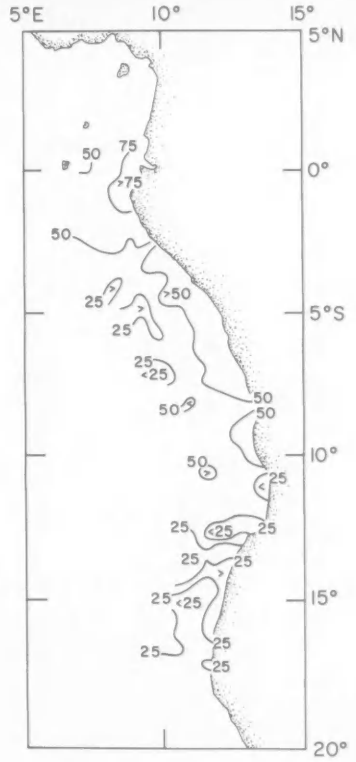

FIGURE 10.—Depth (meters) to the 26.0 g/l σ_t surface from *Undaunted* and *Rockaway* data, October-November 1968.

best be demonstrated with the data collected in October-November, involving 49 sightings with relevant oxygen data. After grouping the oxycline depth measurements into 5-m classes and plotting a sighting versus depth-frequency bar graph (Figure 12), it appears that a smooth inverse relationship exists for depths >10 m. By assigning the central value of each depth class to each sighting in the class, a least squares linear "equation" can be obtained for sighting frequency as a function of oxycline depth in the form:

$$s = a + mz \qquad (1)$$

where s = the number of sightings
z = the depth of the 3.5 ml/l surface
a and m = constants, in this case, equal to 23.15 and −0.59, respectively, leading to

$$s = 23.15 - 0.59z \qquad (2)$$

as the "equation." Note that the equation is defined only over the range of depths from 11 to 40 m. At depths greater than this, school sightings may be difficult to make and at depths less than this the fish may avoid the thin habitable layer.

Although the relationship portrayed in the bar graph appears to be nonlinear, the errors introduced by interpolation between sampling bottle depths and the arbitrary assignment of central values to the frequency classes make any attempts to obtain a best-fit, nonlinear "equation" unwarranted. The linear relationship shown above is about all the sophistication the data will bear, particularly in view of the small number of fish school sightings.

To further pursue the role of environmental conditions in influencing the distribution of skipjack tuna, we considered the concept of habit layer

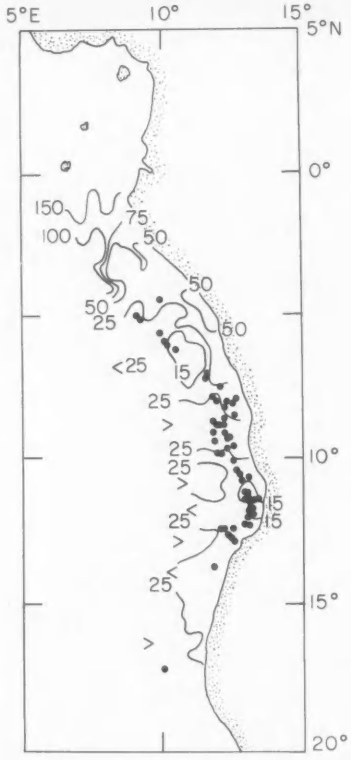

FIGURE 11.—Location of sightings of schools of skipjack tuna during October-November 1968 plotted on the observed oxycline (3.5 ml/l) topography.

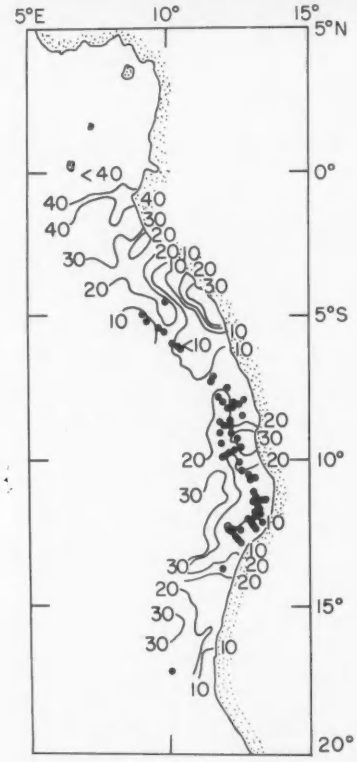

FIGURE 13.—Location of sightings of schools of skipjack tuna (dots) and habitat thickness (meters) from *Undaunted* and *Rockaway* data, October-November 1968.

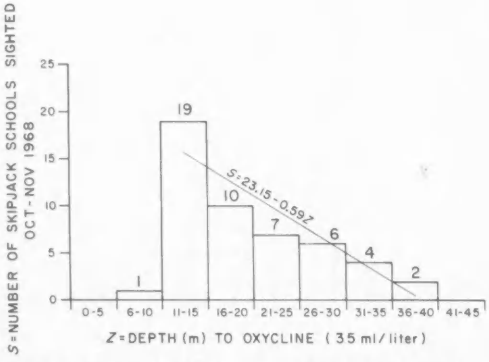

FIGURE 12.—Relationship between skipjack school sightings and oxycline depth from *Undaunted* and *Rockaway* data for October-November 1968.

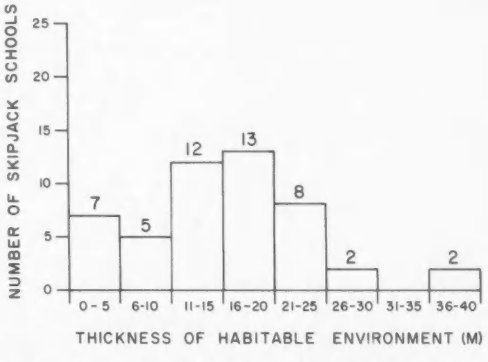

FIGURE 14.—Relationship between skipjack school sightings and habitat thickness from *Undaunted* and *Rockaway* data for October-November 1968.

developed by Barkley et al. (see footnote 4). They defined the habitat of adult skipjack to be bounded above by the sea surface or 22°-26°C (for 9- to 4-kg fish) and below by 18°C or 3.5 ml/l oxygen concentration, whichever is shallower. We plotted the skipjack tuna school sightings on a horizontal chart of habitat layer thickness (using 24°C) for the October-November cruise period (Figure 13). The distribution of school sightings at various habitat layer thicknesses (Figure 14) is considerably different from that at various oxycline depths. Many points in the school sightings versus oxycline depth plot (Figure 12) have shifted to shallower classes in the school sighting versus habitat thickness plot, including seven observations in habitat thicknesses of 5 m or less. This shift is the consequence of regarding the 18°C isothermal surface as the floor of the habitat when it is shallower than the oxycline and assuming that it has a constraining effect equal to that of the 3.5 ml/l oxygen surface. The validity of this assumption is unknown, but comparison of the two distributions (Figures 11, 13) suggest that the 3.5 ml/l oxygen surface has a stronger effect on the skipjack tuna than the 18°C isothermal surface.

The question of whether it is school distribution or availability (to a fishing method) which has been related to oxycline depth cannot be resolved without an independent assessment of tuna school distribution by a different method. The means used to locate tuna schools is essentially that employed by crews of purse seiners and live-bait boats; a watch is maintained for bird activity above feeding or "breezing" schools. This technique reveals only those schools which are available to seines or pole-and-line fishing methods, hence it would be more accurate to consider the factor portrayed in Equation (2) as availability rather than distribution. Those fish not closely approaching the surface would not be detected and would not be available to these harvesting methods.

The pragmatic significance of the relationship between skipjack tuna school availability and oxycline depth lies in its use by fishermen and fishery scientists, the former for more efficient harvest strategy and the latter for more accurate resource assessment. The coincidence of the oxycline and thermocline should provide a very strong lower barrier to downward excursions of tropical tunas, perhaps even strong enough to prevent an encircled school from escaping by sounding before the seine is pursed. If this were true, the efficiency of capture by purse seine would be greater in waters containing a shallow oxycline.

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NOTES

THE SOURCE OF COBALT-60 AND MIGRATIONS OF ALBACORE OFF THE WEST COAST OF NORTH AMERICA

Cobalt is an integral part of the vitamin B_{12} complex and an important cofactor in enzyme systems (Lowman et al. 1971; Reichle et al. 1970). It is, therefore, an element whose cycle in oceanic ecosystems is of interest. The artificial radionuclide cobalt-60 (^{60}Co) has been observed in the livers of albacore, (*Thunnus alalunga* Bonnaterre) collected off the west coast of North America, Washington to Baja California (Pearcy and Osterberg 1968; Hodge et al. 1973).

The albacore is a commercially important migratory species of tuna which normally inhabits the epipelagic subtropical and transitional waters of the Pacific, Atlantic, and Indian oceans. In the North Pacific, albacore may undertake transpacific migrations between Japan and the west coast of America (Clemens 1961; Otsu and Uchida 1963; Clemens and Craig 1965).

While single-pass nuclear reactors were operated at Hanford, Wash., the Columbia River was an important source of artificial radionuclides in the Pacific Ocean off Oregon and Washington. Some radionuclides, formed by neutron activation of impurities in river water used to cool the reactors, were transported via the Columbia out into the ocean and were detectable in the plume water far at sea (Osterberg et al. 1965). Cobalt-60 was among the radionuclides carried by the Columbia River effluent (Gross and Nelson 1966). Fallout from nuclear detonations, however, was another source of ^{60}Co (Lowman and Ting 1973; Hodge et al. 1973). Which of these sources was more significant in contaminating tuna is not known. We shall attempt to use the temporal and geographical variations in ^{60}Co content of albacore livers to estimate the relative importance of the two sources and to provide information on migrations of albacore.

Methods

During the period June–October of 1963 through 1969, over 200 albacore livers were removed from fish (520–850 mm fork length, $\bar{x}$ = 640 mm) collected on surface jigs and preserved aboard ships either by freezing or with Formalin.[1] In the laboratory, livers were weighed, dried, ashed (500° to 570°C), ground, and packed into 15-cm^3 plastic counting tubes for radioanalysis. Samples were counted for 100 min using a 12.7-cm^2 NaI (Tl) crystal detector with a 512 channel pulse-height analyzer. See Pearcy and Osterberg (1968) for additional details on collection and analysis. Results are expressed in picocuries per gram wet weight to be compatible with other published results on cobalt in tuna livers.

Results and Discussion

Concentrations of ^{60}Co in the livers of albacore caught in three general regions along the west coast of North America are shown in Figure 1 for 1964. Of all the years, 1963–69, this year provided the most data for inter-regional and temporal comparisons. Two general trends are evident:

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

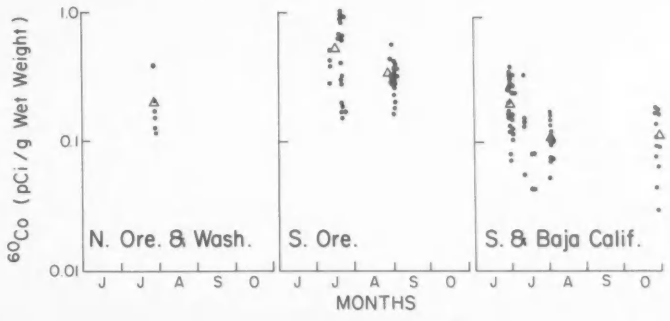

FIGURE 1.—Cobalt-60 concentrations (dots = actual observations, open triangles = $\bar{x}$ values) from livers of albacore captured off three west coast regions during June-October 1964.

first, relatively high ^{60}Co activities were seen off the southern Oregon coast and somewhat lower concentrations off northern Oregon and Washington as well as off southern and Baja California; second, ^{60}Co concentrations decreased with time during the summer–fall period. Data from other years corroborated these trends.

Annual variations of ^{60}Co in albacore off the Oregon coast (dots and solid line in Figure 2) indicate that ^{60}Co concentrations increased from 1963 to 1964 then declined steadily until 1967, but increased again in 1968.

There are two possible sources of ^{60}Co for albacore in the northeastern Pacific. Until 1965, eight Hanford reactors were a relatively constant source of ^{60}Co entering the Columbia River (Gross and Nelson 1966). In 1965, however, a sequence of shutdowns of individual reactors began (Foster 1972). The other possible source of this isotope is fallout from atmospheric tests of nuclear weapons which also varied in time, but according to a different pattern (Lowman and Ting 1973; Hodge et al. 1973). Inputs of ^{60}Co into the environment by atmospheric tests that could directly effect the activity levels in the North Pacific include over 100 U.S. and U.S.S.R. tests in 1961–62 and Lop Nor, China, tests in 1964–65 (one test each year), 1966 (three tests), 1967 (two tests), and 1968 (one test) (U.S. Environmental Protection Agency 1960–72).

The relatively constant input from the Hanford plant fails to account for the low ^{60}Co values observed in albacore during 1963 nor the increased values in 1964 (Figure 2). Other evidence indicating that Hanford was not the major ^{60}Co source is based on our knowledge of the migration of albacore into the Pacific Northwest fishery and their subsequent movements. Albacore often first appear off the southern Oregon coast and move northward and inshore as the summer progresses (Powell et al. 1952; Keene 1974), sometimes along the axis of the warm Columbia River plume waters (Pearcy 1973). Levels of ^{60}Co did not increase with residence time of albacore in Oregon waters or proximity to the Columbia River in northern Oregon (Figure 1), as would be expected if Hanford was the main ^{60}Co source.

These trends are opposite of those noted in albacore livers for ^{65}Zn, a radionuclide that was known to be associated with the Columbia River effluent, but are similar to those of ^{54}Mn, a radionuclide associated with atmospheric fallout (Pearcy and Osterberg 1968). We conclude, therefore, that most of the ^{60}Co we find in albacore livers was

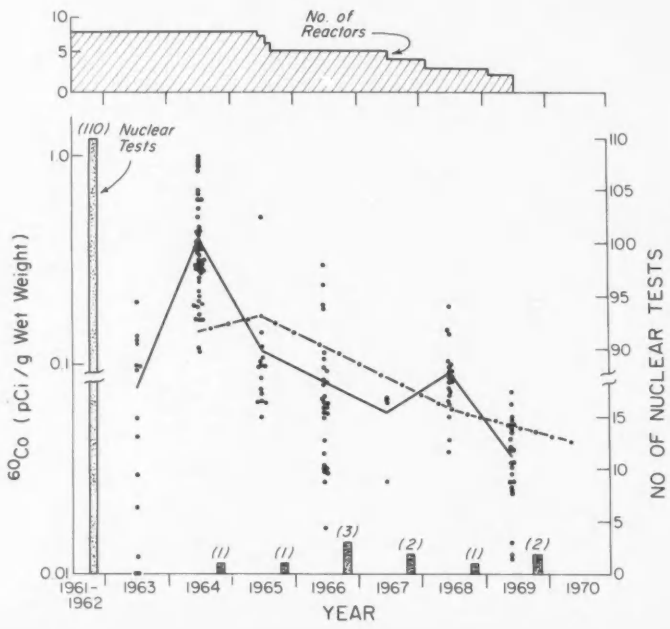

FIGURE 2.—Concentration of ^{60}Co in livers of albacore captured off Oregon and Washington. Solid line indicates mean values of our observations (dots); broken line is a plot of ^{60}Co levels off southern and Baja California as presented by Hodge et al. (1973). Also indicated is the number of Hanford reactors in operation and the number of nuclear atmospheric tests (bars = pre-1963 non-Chinese testing affecting the North Pacific and post-1963 testing at Lop Nor, China) which occurred during our study period.

derived from fallout, even off the coast of Oregon where the influence of the Columbia River plume should be the greatest.

Since radioactivity originating from fallout is higher in the open ocean than in coastal waters where upwelling occurs (Pillai et al. 1964; Folsom and Young 1965; Gross et al. 1965), the spatial-temporal trends evident in Figure 1 may be explained by the residence time of albacore in coastal waters. Highest levels of ^{60}Co are expected in oceanic waters off southern Oregon in June and July; lower levels are expected later in the season after albacore have migrated northward and shoreward and have resided in coastal waters, provided that the biological half-life of ^{60}Co in tuna livers is short enough. The decrease in ^{60}Co levels in albacore (Figure 1) is much more rapid than would be expected from natural radioactive decay of 5.26 yr. Biological turnover must be rapid in order to produce a short effective half-life.

Hodge et al. (1973) related the levels of ^{60}Co in albacore to fallout deposition and found that maximum uptake of ^{60}Co by albacore lagged nuclear atmospheric detonations by 1–2 yr. Annual changes of ^{60}Co concentrations observed off Oregon (Figure 2) show a similar delayed response, but the peak activity levels in albacore occurred a year earlier than the peaks seen by Hodge et al. (1973) off southern California (dashed line, Figure 2). The main atmospheric input by nuclear detonations occurred in 1961–62. Our main peak of ^{60}Co in albacore occurred in 1964, and that reported by Hodge et al. occurred in 1965, indicating a delay of about 2 and 3 yr respectively after testing before the uptake is observed in albacore. This not only suggests that the source of ^{60}Co in albacore is from atmospheric fallout, but that the availability of the radionuclide was different between the albacore caught off California and those caught off Oregon, perhaps because of differences in distributions and migratory patterns than those described by Clemens (1961).

Laurs and Lynn (1977) presented data that confirm this suggestion. Based on recapture of tagged albacore and length-frequency distributions, they concluded that the albacore population found off Oregon is different from that found off southern and Baja California. They further suggest that albacore which migrate into Oregon waters may come from a portion of the offshore population which is located north of the 35th parallel, while those that move into the California waters are located south of the 35th parallel.

The bomb detonations at Lop Nor (lat. 40°N) gave the heaviest fallout input into the North Pacific at about this latitude. Due to the circulation in the North Pacific (Sverdrup et al. 1942), it appears quite possible that albacore which were associated with waters north of lat. 35°N may have experienced high levels of ^{60}Co up to a year before the tuna associated with waters to the south. Circulation in the North Pacific and the latitudinal differences in the location of the two portions of the albacore population appear to be a plausible explanation for the difference of 1 yr in activity peaks between albacore caught off Oregon by us and those off southern and Baja California by Hodge et al. (1973).

Acknowledgments

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LENGTH–WIDTH–WEIGHT RELATIONSHIPS FOR MATURE MALE SNOW CRAB, *CHIONOCOETES BAIRDI*

Snow crabs have been exploited commercially in Alaska since 1961 (Alaska Department of Fish and Game 1975). *Chionocoetes bairdi* is the predominant species with *C. opilio* composing up to 25% of the catch from the Bering Sea. Landings were small and intermittent in the early 1960's but increased to about 3.2 million lb in 1968. Landings expanded dramatically thereafter and exceeded 60 million lb in 1974, with an ex-vessel value of more than $12 million.

Carapace width measurements have been collected from the commercial snow crab catch by biologists since the inception of the fishery; individual weights, however, are not routinely collected because the task is rather time-consuming. The relationships between carapace width, length, and body weight are of interest to biologists and processors. The relationship between carapace length and width is of interest because the carapace shape is one of the diagnostic characteristics to distinguish between *C. bairdi* and *C. opilio* and hybrids of the two species (Karinen and Hoopes 1971). The relationships between carapace width and weight and carapace length and weight have many uses. They are, for example, indicators of condition, used to calculate biomass, and used to estimate recovery of edible meat from crabs of various sizes.

Materials and Methods

Carapace length and width and body weight measurements were taken from 240 mature male *C. bairdi* from commercial catches made south of the Alaska Peninsula in the vicinity of the Shumagin Islands in May 1975. Length and width measurements were taken to the nearest millimeter with vernier calipers and weights were recorded to the nearest gram. Length was measured from the posterior medial edge of the carapace to the anterior medial point of the right orbit. The rostrum was not included in the length measurement because it often erodes when crabs are carried in the live tank of fishing vessels. Width was measured at the widest part of the carapace and included the lateral branchial spine. Width ranged from 128 to 185 mm, weights from 635 to 2,230 g, and lengths from 92 to 143 mm.

The basic linear regression formula $W = a + bL$ was used to express the relationship between width (W) and length (L). Weight (Wt) was related to width and length by the power functions, $\log_{10} Wt = \log_{10} a + b \log_{10} W$ and $\log_{10} Wt = \log_{10} a + b \log_{10} L$. The constants a and b were determined empirically.

Results

The length–width, length–weight, and width–weight relationships are summarized in Table 1. All relationships were characterized by very high correlation coefficients. No relationships between length, width, and weight have previously been reported for *C. bairdi*.

TABLE 1.—Length–width, length–weight, and width–weight relationships for mature male *Chionocoetes bairdi*. [Sample size was 240 animals for each relationship.]

Relationship	Coefficient	Formula
Length–width	0.96	$W = -3.584 + 1.268L$
Length–weight	0.99	$\log_{10} Wt = -3.076 + 2.956 \log_{10} L$
Width–weight	0.99	$\log_{10} Wt = -3.363 + 2.936 \log_{10} W$

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TEMPORAL ASPECTS OF CALLING BEHAVIOR IN THE OYSTER TOADFISH, *OPSANUS TAU*

The oyster toadfish, *Opsanus tau* (Linnaeus), produces two calls: an agonistic grunt and a boatwhistle associated with courtship (Fish 1954; Tavolga 1958, 1960; Gray and Winn 1961). The boatwhistle is produced only by males on nests (Gray and Winn 1961) and is endogenously driven as well as influenced by calling of surrounding males (Winn 1964, 1967, 1972; Fish 1972). A toadfish, not hearing other males, may still boatwhistle for long periods and attract a female. Although toadfish may be influenced to call by the calling of adjacent males, one would assume the circadian patterning of the boatwhistle to be influenced by photoperiod and the fish's behavioral strategy relative to it. Additionally, the rate of calling may be a key to a male's internal state. Calling rate has been manipulated experimentally (Winn 1967, 1972; Fish 1972; Fish and Offutt 1972), but no one has studied the calling rate of undisturbed individual fish. This note is a preliminary attempt to look at these twin problems (when and how fast toadfish call) by recording the boatwhistles of individual males on their nests.

Materials and Methods

Terra cotta drainage tiles were set out individually adjacent to the pilings of a dock at Solomons, Md. Male toadfish which settled into three of the tiles started calling, and the calls were monitored between 9 and 15 June 1969. Because of changing tapes and mechanical problems, the record was not continuous. The recording system consisted of individual Clevite[1] oyster (CH 15-J) hydrophones with their own General Electric Phono-Mic preamplifiers (UPX-003C) and a Precision Instrument Model 207 multichannel tape recorder. The gain was turned down so that only boatwhistles from the fish in the tile adjacent to the hydrophone would present a loud signal. The tapes were transduced onto strip chart paper (Bruel and Kjaer level recorder type 2305), and segments equivalent to 6 min of real time were continuously marked on the chart paper. The number of boatwhistles in each segment was counted.

Results

The activity patterns for the three fish appear aperiodic (Figure 1; Table 1). All of the animals called both day and night (11 calling periods day, 9 night), and the total number of boatwhistles produced for day and night was similar (7,905 day, 6,202 night). Considering the data on a calls-per-hour basis, since daylight hours exceed nighttime in June, does not appreciably alter the results. The fish averaged 41.3 boatwhistles/h during the day and 46.1/h at night from recordings covering 191.5 h of daylight and 134.5 h of darkness. Not only were crepuscular peaks absent, but dawn and dusk appeared irrelevant as cues for calling behavior. There are similarities between certain periods in the data, such as the nights of 14 and 15 June for channel 2, but these similarities are a

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

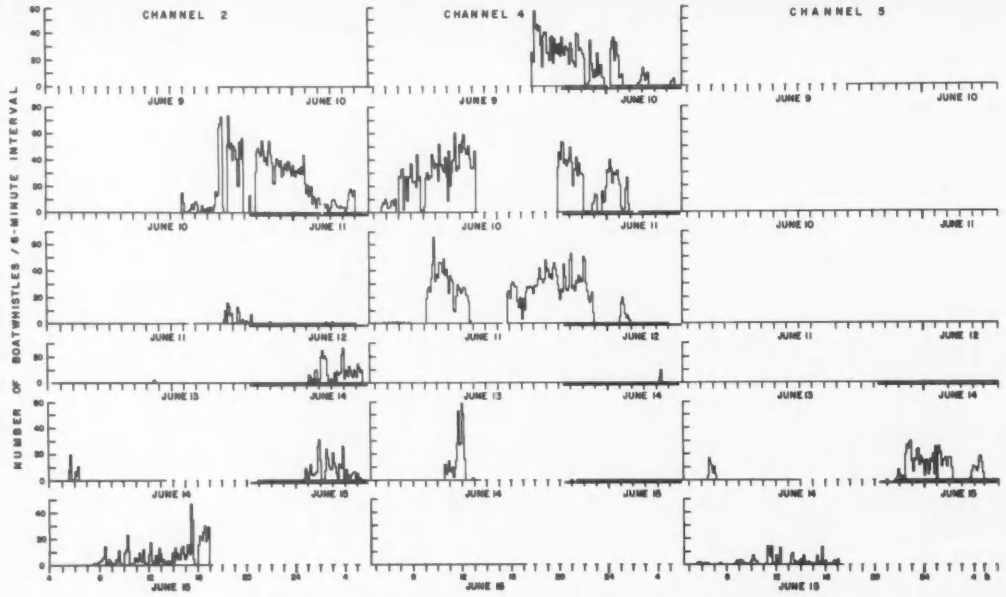

FIGURE 1.—Temporal record of boatwhistle production for each of three toadfish. A missing baseline indicates gaps in the record, and the horizontal line below the baseline indicates the period of darkness.

TABLE 1.—Number of boatwhistles produced during 24-h periods by three toadfish.
[L is light, D is dark, and dash indicates no data.]

Date	Channel 2		Channel 4		Channel 5	
	L	D	L	D	L	D
June 9-10	0	0	849	951	0	0
10-11	890	1,838	2,315	1,103	0	0
11-12	87	11	2,435	848	0	0
13-14	4	364	0	14	0	0
14-15	51	354	355	0	63	719
15	650	—	0	—	206	—
Total	1,682	2,567	5,954	2,916	269	719
Periods called	5	4	4	4	2	1
Total D/total L	1.53		0.49		2.67	

minor feature of the record. Each of the fish produced different numbers of boatwhistles and exhibited separate patterns of calling (Figures 1, 2; Table 1) that were not obviously correlated with each other. One fish (channel 4) boatwhistled twice as much during the day as at night, while the other two (channel 2 and 5, respectively) called 1.5 and 2.7 times more at night than during the day. These ratios from Table 1 change to 2.24, 0.66, and 3.92, respectively when considered on a per-hour basis.

In order to see how fast individual fish called, we constructed histograms of the frequency of occurrence of number of boatwhistles in the 6-min segments (Figure 2). Even though the distributions for day and night were statistically different (Kolmogorov-Smirnoff test), they were combined in each of these histograms. Since these day-night differences have already been mentioned and were inconsistent between fish (Table 1), it seemed reasonable to present differences between the fish rather than differences between day and night.

Data from the three channels were combined to show the calling rate from all boatwhistles recorded in this study (Figure 3). It is obvious that toadfish remain quiet for long periods (Figure 1). For Figures 2 and 3, all quiet periods of 60 min or longer were arbitrarily excluded. Still, zeros accounted for close to 20% of all intervals measured (Figure 3). From the cumulative percent curve (Figure 3), it is striking how strongly the distribution is skewed toward the low end. Over 50% of the intervals measured had ≤ 1 to 2 boatwhistles/min (ca. 10 calls/6 min), and over 75% of the intervals had ≤ 4 to 5 boatwhistles/min. Only 10% of the intervals contained calls emitted at a rate of 6 or more per minute. Finally less than 1% of the intervals contained calls emitted at a rate of 10 to 12/min. Although an animal may have called for

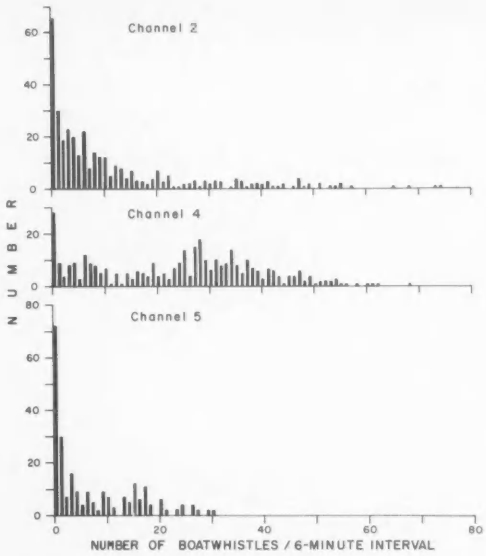

FIGURE 2.—Histogram of frequency of occurrence (i.e., "number" on Y-axis) of number of boatwhistles in 6-min intervals (X-axis) for each of three toadfish. Silent periods of an hour or longer were excluded from the analysis.

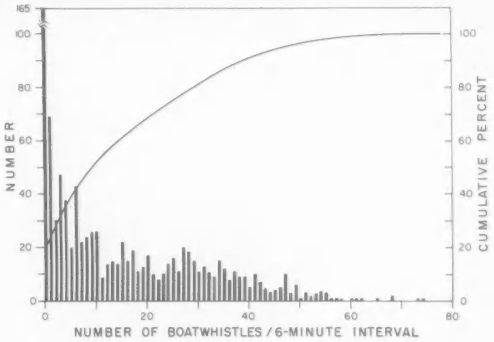

FIGURE 3.—Histogram of frequency of occurrence (left axis) and cumulative frequency of occurrence (right axis) of number of boatwhistles in 6-min intervals combined for the three toadfish. Silent periods of an hour or longer were excluded from the analysis.

many hours (Figure 1), the number of calls fluctuated markedly. High rates of calling were often strongly peaked, i.e., not maintained for long periods.

Discussion

The only obvious feature of the data from this study (Figure 1; Table 1) is its lack of patterning or predictability. Clearly, the recordings indicate no diel cycle. While they do not rule out the possibility of maximal or minimal periods of sound production for a toadfish population (Breder 1968), it appears unlikely that individuals would be synchronized to any great degree. It is difficult to reconcile these results with the periodicity of the in-air respiration data of Schwartz and Robinson (1963) and the impressions of Tavolga (1960) and Schwartz and Robinson (1963) that the toadfish is basically nocturnal. Squirrelfishes are active at night, when they are least vocal (Winn et al. 1964; Salmon 1967; Bright 1972; Bright and Sartori 1972), and likewise toadfish might not have a clear vocalization rhythm, while maintaining rhythms for respiration or other functions.

The rate of calling by fish in this study was low, and individuals lapsed into silence for long periods. This result verifies our experience from playback studies (Winn 1967, 1972; Fish 1972; Fish and Offutt 1972); fish were often silent, forcing us to sample many tiles to find a male calling rapidly enough for use in an experiment. For this reason preplayback calling rates, equivalent to control calling rates, were biased upward. From 68 experiments, each with sample sizes ranging between 11 and 16, Winn's (1972) preplayback data (recalculated) show a mean of 22.41 ± 4.3 (1 SD) boatwhistles/3 min, or an average of 7.5 calls/min. In his initial playback experiments, Winn (1967) increased the calling rate to an average of 11.46, 11.70, and 11.48 boatwhistles/min by playbacks of 18, 26, and 36 boatwhistles/min. Playbacks of 10 calls/min did not increase calling. Fish (1972) found that with optimally spaced playbacks, he could increase their rate to 14 to 16 sounds/min (1 call every 3.7 to 4.3 s). He called this pace the maximum sustained calling rate. Fish's data combined with Winn's indicate that when competing with other males, the toadfish does not grade his output uniformly, but follows more of a step function, i.e., his calling is either facilitated or not. In one chance encounter Fish (1972) observed a male calling 25 times/min as a female approached his shelter.

Our fish called considerably below their capabilities. However, calling rates of 11 and 12/min would suggest that the males were sexually receptive. It will take more work to establish what is normal for the toadfish and what abiotic

and biological factors control motivation during the season. An unspawned male and a once-spawned male guarding eggs, might call at different rates. Schwartz (1974) and Lowe (1975) have indicated spawning peaks, which could be related to calling motivation. Although calling decreases, boatwhistles are still emitted after the assumed mating season (Fine 1976) It is not possible to accurately place the period of 9–15 June 1969 in a spawning peak or lull.

Density within a toadfish population will also affect sound production since calling fish facilitate each other. There could also be a tonic facilitation (Schleidt 1973), so that fish hearing boatwhistles, even if below the stimulatory rate, would be more prone to call than would a solitary male. It is also possible that some populations of toadfish could be limited by shelter availability for male nesting. At the dock at Solomons, where these recordings were made, shelter was provided primarily by our tiles placed along the dock pilings. Since the area was largely clear of rocks, tin cans, and boards which might provide shelter, the density of calling fish in the experimental area was not high, and we might not expect a great deal of facilitation.

Acknowledgments

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BIOLOGY AND HOST–PARASITE RELATIONSHIPS OF *CYMOTHOA EXCISA* (ISOPODA, CYMOTHOIDAE) WITH THREE SPECIES OF SNAPPERS (LUTJANIDAE) ON THE CARIBBEAN COAST OF PANAMA

Although parasitic isopods of the family Cymothoidae have been described from both freshwater and marine fishes, relatively little is known of their biology and host–parasite relationships (Morton 1974). Probably all species of cymothoids are protandrous hermaphrodites, with the male larvae settling out of the plankton onto the mouth, body surface, body cavity, or gills of their host. After a period of maturation, males of some species become associated with the buccal cavity where they undergo a sex change. Both broad and limited host specificities have been described for members of the Cymothoidae (Trilles 1964).

Here we comment on the biology and occurrence of *Cymothoa excisa* Perty on three sympatric species of Caribbean snappers: *Lutjanus synagris* (Linnaeus), *L. analis* (Cuvier), and *Ocyurus chrysurus* (Bloch). Host–parasite relationships and infestation rates are discussed and evidence is provided suggesting that this parasite does little, if any, damage.

Methods and Materials

All specimens were collected along the Caribbean coast of the Republic of Panama and the Canal Zone, near the Smithsonian Tropical Research Institute's Galeta Marine Laboratory. Samples were taken in sea grass habitats consisting primarily of *Thalassia testudinum*, using a 4.9-m otter trawl with 1.3-cm bar mesh. Details of the trawling program and site descriptions are given in Heck (in press). All material was sorted in the laboratory and subsequently preserved in 10% Formalin.[1]

Fishes from which parasites had been removed were wet weighed after blotting. Standard lengths of fishes were measured to the nearest 0.5 mm, and total lengths and widths of isopods were measured to the nearest 0.01 mm, using dial calipers. Individual isopods were sexed according to the presence of an appendix masculina on the second pleopod (males) or from the development of oostegites and presence of larvae (females). The Montalenti femininity index [F.I. = $W/L \times 100$, where W = width and L = length (Montalenti 1941)] was used for the isopods as a measure of the degree of transformation from male to female.

Fulton's coefficient of condition [$K = W/L^3$, where W = wet weight and L = standard length (Ricker 1971)] was used to assess the well-being of fish in relation to the presence or absence of isopods. Values of K were computed for 30 infested and 30 isopod-free individuals in each of the three species of snappers, *L. synagris*, *L. analis*, and *O. chrysurus*. An arc–sin transformation was performed on K values before statistical analyses were carried out.

Results and Discussion

Cymothoa excisa was found to occur on 4.7% (32/681) of the *L. synagris*, 10.5% (16/152) of the *L. analis*, and 2.1% (11/527) of the *O. chrysurus* collected. Adults of the two snapper genera exhibit different habitat preferences: members of the genus *Lutjanus* prefer near-bottom habitats with ample cover, while *O. chrysurus* inhabits the open-water column above coral reefs. Juveniles of all three species are commonly associated with sea grass beds, and it may be during this stage of their life cycle that infestation occurs. This is suggested by the occurrence of metamorphosed parasites in very small fish (20–30 mm SL). In addition, a linear relationship exists between lengths of the isopod and those of its host (Figure 1), which further suggests that fishes are infested early in life with subsequent growth by both host and parasite. Six male parasites differed significantly from this relationship, however, and each of these occurred jointly (or in triplicate) with a much larger female. Previously, Bowman (1960) reported that pairs of isopods (*Lironeca puhi* Bowman) were nearly always present in the gill cavity of the moray eel *Gymnothorax eurotus* (Abbott). In our specimens, pairs (or triplicates) were found in only 6.8% of the parasitized fishes and during sorting no free isopods were found which might have escaped from the mouth cavity. Unless male isopods were differentially lost during the trawling operations, it appears that the population biology of cymothoid genera can be quite different.

Several other species of lutjanids collected showed no indication of isopod infestation. For example, none of the 53 *Lutjanus griseus* (Linnaeus) nor any of the 19 *L. apodus* (Walbaum) contained *C. excisa*. Differences in habitat prefer-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

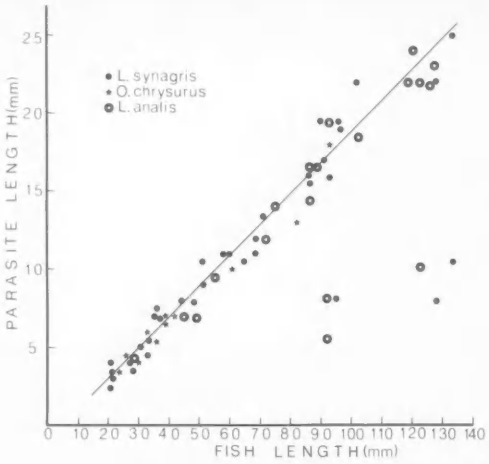

FIGURE 1.—Relationship between *Cymothoa excisa* and lutjanid lengths. Least squares line was fit excluding the six points which fall far below the cluster of other points. These six points represent males which occurred jointly with females.

ences may be responsible for the absence of cymothoids on these species. It is also possible that nonparasitized snapper species are cleaned of parasites by cleaner fishes and decapod crustaceans on nearby reefs.

All isopods were attached to the tongue and oriented anteriorly with smaller males positioned behind females. Some degeneration and possibly some scar tissue were evident at the base of the tongue, but not elsewhere in the mouth. The mouth parts of *C. excisa* seem adapted for piercing and sucking and Morton (1974) has postulated that cymothoids are hemophages. As expected, females of *C. excisa* are proportionately wider than males, and the transition from male to female appears to occur in the 13- to 19-mm size range (Figure 2).

Bowman (1960) presented evidence that the presence of a female suppresses feminity in cooccurring males, as expressed by the Montalenti index. We found just the opposite result: males occurring jointly with females displayed a significantly higher average femininity index than males which occurred alone (Figure 2); (t-test, $P<0.01$). The reason for this difference is unknown.

Because *C. excisa* filled so much of the mouth cavity of infested snappers, it seemed, a priori, that the presence of isopod parasites must interfere with feeding. However, several crustacean families, including Xanthidae (*Micropanope* sp., *Pilumnus* sp., *Panopeus* sp.), Porcellanidae (*Petrolisthes* sp.), Squillidae (*Squilla* sp.), Penaeidae (*Penaeus* sp.), and Alpheidae (*Alpheus* sp.), were represented in the gut contents of the infested snappers. Moreover, there were no significant differences between coefficients of condition calculated for parasitized and unparasitized fish in any of the three lutjanids (t-test, $P = 0.01$). Thus it appears that any harmful effects due to the presence of parasites are not reflected in either the ability to capture prey or in overall health, as measured by K. It is possible, however, that the presence of isopod parasites may lower fitness by causing increased mortality during periods of stress (Keys 1928), by reducing the reproductive output of infested fish, or by decreasing the ability of parasitized individuals to avoid predators. Although the requisite data are lacking to test the first two premises, we were able to test the latter possibility indirectly using the following reasoning: If predation is not selective for parasitized individuals, then a similar distribution would be expected for each group. This was tested by assigning both parasitized and nonparasitized individuals of all three species to 20-mm (SL) size classes for all but the largest fish (excluded because of small sample size). There was no significant difference between the two groups ($\chi^2 = 6.69$, $P = 0.05$).

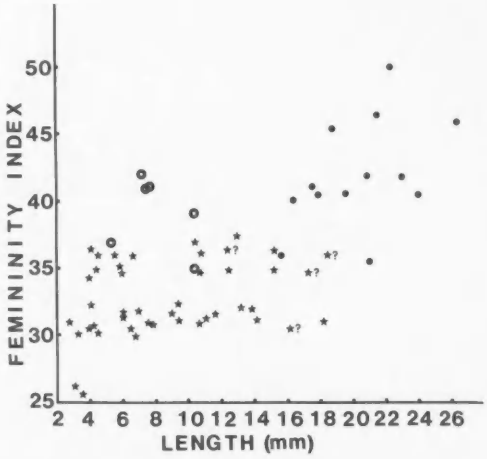

FIGURE 2.—Femininity index in *Cymothoa excisa*. Legend: * = male, • = female, o = male occurring jointly with female, *? = sex indeterminate.

On the basis of these results and the data previously presented, we consider *C. excisa* to be a relatively benign parasite. This appears to be a general characteristic of host–parasite relationships between cymothoids and fishes, at least in unstressed situations (Keys 1928).

Acknowledgments

Specimens of *C. excisa* were kindly identified by T. Bowman, U.S. National Museum of Natural History (USNM), and have been deposited at the USNM. C. M. Courtney, Marco Ecology Laboratory, Marco Island, Fla., sexed the parasites and analyzed gut contents of parasitized fishes. D. T. Logan and M. H. Baslow provided comments on the manuscript.

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FECUNDITY OF THE SOUTHERN NEW ENGLAND STOCK OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*

The yellowtail flounder, *Limanda ferrunginea*, is an important commercial species to both the New England and Canadian fishing industries. According to Royce et al. (1959) there are five relatively distinct stocks of yellowtail flounder with little migration occurring between them: southern New England, Georges Bank, Cape Cod, Nova Scotian, and Grand Bank stocks. Catches have recently been declining. For example in the southern New England and Cape Cod stocks (ICNAF (International Commission for the Northwest Atlantic Fisheries) subarea 5Zw), the number of metric tons landed per standard fishing day has declined from 3.5 in 1970 to 1.5 in 1975; the total catch declining from 24,103 to 5,460 metric tons over the same period (Cain[1]).

Pitt (1971) has estimated the fecundity of the Grand Bank stock (ICNAF Subareas 3L, 3N, 3O) but no other yellowtail flounder fecundity data have been published. Fecundity may vary from one stock of flatfish to another, e.g., plaice (Simpson 1951), so we have analyzed the fecundity of the southern New England stock of yellowtail based on 50 fish, and compared these values with the fecundity estimates of Pitt (1971).

Methods and Materials

Ovaries used for fecundity estimates were collected on 9 and 12 April 1976 from fish landed by commercial vessels at Point Judith, R.I. Fish were randomly sampled from the combined catches of several vessels, and therefore represented a random sample of the southern New England population. Only ripening ovaries, i.e., ovaries swollen but eggs not fully developed in size (Scott 1954), were used thus omitting fish that may have begun to spawn. Fish were measured to the nearest centimeter total length, and the ovary wet weight was determined to the nearest 0.1 g. Ovaries were preserved in Gilson's fluid as modified by Simpson (1951) and allowed to remain in this solution for 3-5 mo to facilitate ovarian tissue breakdown. Otoliths, read independently by each of us, were used to determine ages. The growth rings were recognized according to Scott (1954) who also

[1]Cain, W. L. 1976. Yellowtail flounder tabulations for 1977 assessments. Int. Comm. Northwest Atl. Fish. Working Pap. No. 76/IV/49.

demonstrated the validity of the use of otoliths for the age determination of yellowtail flounder.

Eggs were separated from the ovarian tissue by washing with a gentle stream of water through a series of four fine mesh screens (mesh sizes 1.52, 0.98, 0.51, 0.14 mm). After separation the eggs were placed in a gallon jar and diluted with water to 3,000 ml. Large samples were first divided using a plankton splitter and only half of the sample diluted. The lid of the gallon jar was modified to hold a 1-ml Hensen-Stemple pipette which extended approximately 15 cm into the jar. The jar was then inverted 10 times and the sample taken before any settling of the eggs occurred. The subsample was placed onto a gridded Petri dish and the eggs counted with a dissecting microscope. A minimum of three subsamples were counted for each fish. The coefficient of variation was computed and ranged from <1 to 18% (mean = 7.5%). Fecundity was estimated by multiplying the mean number of eggs from the subsamples by 3,000, or 6,000 if the sample had been split.

Results and Discussion

Linear regressions, correlation coefficients (r), and coefficients of determination (r^2) were computed from data transformed to common logarithms. These were:

$$F = 0.986L^{3.858} \quad \text{(Figure 1)} \quad (1)$$
$$r = 0.885,\ r^2 = 0.784$$

$$F = 240{,}700A^{1.294} \quad \text{(Figure 2)} \quad (2)$$
$$r = 0.812,\ r^2 = 0.659$$

$$F = 62{,}150G^{0.678} \quad \text{(Figure 3)} \quad (3)$$
$$r = 0.941,\ r^2 = 0.885$$

were F, L, A, and G are fecundity (10^6 eggs/female), length (centimeters), age (years), and gonad weight (grams), respectively. In all equations the slopes were significantly different from zero ($P < 0.001$).

The coefficient of determination for Equation (3) shows that 88.5% of the variation in fecundity was related to gonad weight independent of both length and age. This was more than the variation related to length alone (78.4%, Equation (1)) or age alone (65.9%, Equation (2)). Furthermore, the correlation coefficient for fecundity vs. gonad weight was significantly higher than that for fecundity vs. length ($t = 3.85$, df = 47, $P < 0.001$), and fecundity vs. age ($t = 4.84$, df = 47, $P < 0.001$). Gonad weight, therefore, contributed most to the variation in fecundity and would be the best parameter to measure in estimating fecundity. However, since the relationship between ovary weight and fecundity varies seasonally, depending on the stage of development, this conclusion may be valid only for prespawning fish.

In addition to the 50 pairs of ovaries collected by us, we estimated the fecundity of 14 fish (lengths 29-46 cm, ages 2-6 yr) from the southern New England stock collected in 1976 by the Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass. The regression lines for fecundity vs. length and fecundity vs. age for these fish were not significantly different ($P > 0.25$) from our regressions when compared

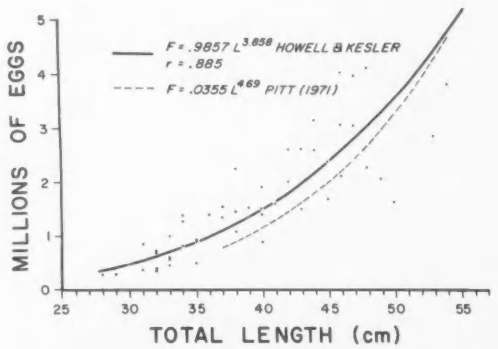

FIGURE 1.—Yellowtail fecundity plotted against length. Solid line is the fitted curve for the southern New England population, and the dashed line that of the Grand Bank population.

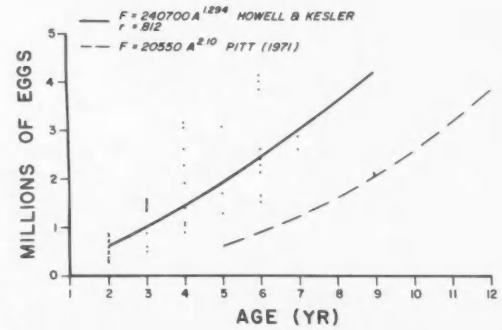

FIGURE 2.—Yellowtail fecundity plotted against age. Solid line is the fitted curve for the southern New England population, and the dashed line that of the Grand Bank population.

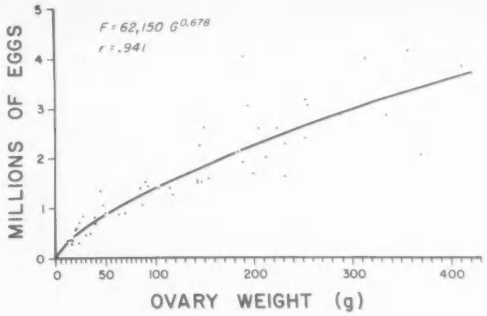

FIGURE 3.—Yellowtail fecundity plotted against ovary weight, and the fitted curve for southern New England.

using an analysis of covariance (Snedecor and Cochran 1967).

We compared our data with those of Pitt (1971) for the Grand Bank stock (lengths 37-54 cm, ages 5-12 yr) using analysis of covariance. The slopes of fecundity vs. length and fecundity vs. age regression lines were not significantly different ($P > 0.25$) (Figures 1, 2). This indicates that the rate with which fecundity increased with both length and age was not significantly different between the two populations. However, the intercepts of the fecundity vs. length regressions were significantly different ($F = 8.67$; df = 1, 94; $P < 0.01$), southern New England fish being more fecund for a given length than Grand Bank fish (Figure 1). In addition, the intercepts of the fecundity vs. age regressions were significantly different ($F = 28.87$; df = 1,92; $P << 0.005$) indicating that southern New England fish were more fecund for a given age (Figure 2).

There may be several reasons why fecundity is higher at a given length and age in the southern New England stock. Several authors including Hodder (1965), Bagenal (1969), and Tyler and Dunn (1976) have suggested that both nutrition and temperature can affect egg production. Little is known about the type and amount of food available to the two populations so no speculation can be made about the possible nutritional effects on fecundity in this species. Water temperatures inhabited by the two stocks are different. Southern New England yellowtail flounder inhabit waters of 4.9–12.3°C (Royce et al. 1959), while Grand Bank yellowtail flounder are found at temperatures of −1° to 6.5°C (Pitt 1974). Pitt (1974) found that the southern New England population grew faster than the Grand Bank population, probably due to these warmer temperatures. This accelerated growth rate apparently results in earlier maturation of the southern New England fish, 50% of the females being mature at 2–3 yr old and 32 cm long (Royce et al. 1959) as compared with 5–6 yr and 37 cm long for Grand Bank females (Pitt 1970). Simpson (1951) found that faster growing plaice were more fecund for a given age and length. Likewise, Pitt (1964) found that in American plaice of comparable ages, ovaries of faster growing fish were larger than those of slower growing individuals, and fecundity was higher. If the ovaries of the faster growing southern New England yellowtail flounder are larger at comparable ages and lengths than those of Grand Bank fish, we would expect southern New England fish to be more fecund, as was the case. The ecological implications of this higher fecundity are unknown and require further study.

Acknowledgments

We thank Robert Livingstone and Judith Penttila of the Northeast Fisheries Center, NMFS, NOAA, Woods Hole, who generously provided us with ovaries and ages of some yellowtail flounder. Thanks go to T. K. Pitt who provided us with the raw data necessary to compare the two stocks, and to S. B. Saila and W. H. Krueger of the University of Rhode Island who critically read the manuscript.

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"MOCK FISH" METHOD FOR STUDYING MICROBIAL INHIBITING AGENTS

In experiments intended to study the effects of various agents or conditions on the microbial outgrowth in food products, it is desirable to approach efficacy similar to those conditions of actual handling and marketing. However, in experiments on fishery products, when one wishes to find effects of an agent or condition, the use of whole fish or fish fillets adds variables to any experimental design. These undesired variables are: variations in the total microbial population and in the composition of the microbial flora from fish to fish; different time intervals and other storage variations in the handling history of fish even from the same catch; different fillet or sample thicknesses which will affect the counts per gram ratio from sample to sample; different physiological conditions, age, wounds, etc., of the fish which might affect experimental comparisons; and possible presence of inherent antibiotics in the substrate. The latter variable does not permit a separation of the antibiotic effects of the additives from the antibiotic effects of the substrate.

In order to study what effects agents might actually have on specific microbial outgrowth in an efficacious situation, a "mock fish," composed of gelatin (containing nutrients) and supported structurally with cheesecloth was devised. The mock fish allowed us to control: total number and composition of the microbial flora; location of microbial contamination, e.g., surface or evenly dispersed throughout the sample; uniformity of distribution of microbes from sample to sample; size and thickness of the samples; and the handling history and physiological state of the samples. This system permits the quantitative recovery of the inoculated microbes by simply melting the gelatin at 31°–32° C.

This note describes the application of mock fish in studying the effects of disodium ethylenediamine tetraacetate (EDTA, Fisher Scientific Co.[1]) with or without an iodophor (Wyandotte Co.) contained in ice for controlling microbial outgrowth of a mixture of four *Pseudomonas* species. This procedure is not recommended as a means of predicting the effectiveness of an inhibitor on a specific species of fish. Its role is to screen inhibiting agents for general effectiveness and to permit a comparison among them.

Materials and Methods

Mixture of *Pseudomonas* Species

Four *Pseudomonas* species, previously isolated from iced fish in our laboratory, were used in these experiments. Each species of *Pseudomonas* was grown in separate Eugon Broth (BBL) test tube culture for 18 h at 20°C. Then 2 ml from each culture were pooled and well mixed in a sterile test tube to prepare an inoculum mixture. From this mixture 1 ml was inoculated into 1 liter of melted gelatin medium described below to give an estimated 10^4 to 10^5 bacteria/ml of the final preparation.

Mock Fish Preparation

1) Cheesecloth discs were cut to size to fit inside glass Petri dishes, and then they were cut in half. The Petri dishes were then sterilized at 121°C for 15 min.

2) Ten milliliters of melted, inoculated 10% gelatin and 1% Eugon Broth medium were pipetted into each sterile Petri dish. A sterile needle was used to make sure that the cheesecloth disc halves did not overlap during gelatin solidifica-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

tion. Once solidified, the gelatin in each plate was cut in half with a sterile needle along the cheesecloth division, thus making two mock fish for use in experimental procedures. The mock fish were gently pried loose from the Petri dish with the aid of a sterile spatula or large, blunt forceps and placed into a beaker containing crushed ice. The cheesecloth provides ample structural support to the solidified gelatin.

Preparation of Crushed Ice

To minimize contamination, distilled water, glassware, ice cube trays, and an ice cube crusher were sterilized prior to use in the preparation of solutions and crushed ice. Using distilled water to minimize the presence of chlorine, minerals, etc., the following solutions were prepared: 1) 1% EDTA; 2) 0.1% EDTA; 3) 1% EDTA plus 1% $CaCl^2$; 4) 0.1% EDTA plus 1% CaCl; and 5) 0.1% EDTA plus 10 ppm of Accord (an iodophore manufactured by BASF Wyandotte Corp., Wyandotte, Mich.).

In order to demonstrate the applicability of this mock fish method, we tested the effect of EDTA embedded in ice on typical *Pseudomonas* species found associated with iced fish. Interest in EDTA for use as a microbial inhibitor has been cited by Levin (1967), Winarino et al. (1971), and Maunder et al.[2] The addition of calcium ions was to interfere with the chelating property of EDTA. The addition of an iodophor was to observe for a possible greater effect.

The control ice contained no added ingredients. These solutions were poured into ice cube trays and frozen. A hand operated individual ice cube crusher was used to prepare crushed ice to fill 800-ml beakers. From 8 to 10 mock fish were placed into each beaker containing crushed ice and stored at 0°C for the duration of the experiment.

Bacterial Assays

At each time interval (0, 1, 3, 6, and 11 days), mock fish were removed from each beaker and placed in a sterile plastic petri dish. The Petri dishes were floated on a 31°–32°C water bath to melt the gelatin. Aliquots of the melted, well-stirred gelatin were decimally diluted and plated using Eugon Agar (BBL) with 0.1% yeast extract (BBL) added. Plates were incubated at 20°C for 5 days prior to counting.

[2]Maunder, D. T., W. P. Segner, C. F. Schmidt, and J. K. Boltz. 1966. Growth characteristics of Type E *Clostridium botulinum* in the temperature range of 34 to 50°F. Annu. Rep. to U.S. At. Energy Comm. (now ERDA), Contract No. AT(11-1)1183.

Results and Discussion

The results of the experiments are shown in Figure 1. The initial starting population was 4.5×10^4 pseudomonads/ml of gelatin medium. The resulting growth patterns reflect the effect of agents contained in the ice and melt water. By the 5th day, melt water entirely surrounded the mock fish in each beaker. By about the 10th day, the floating ice composed one-half to one-third of the beaker contents.

The mock fish held together throughout the experiment with only occasional slivers, not supported by the cheesecloth, breaking off.

The mock fish method permits an evaluation of the effects of microbial inhibiting additives, used singly or in combination, to yield relatively accurate results. Thus, the method may be used to screen a wide variety of antibiotic systems before going into efficacy studies. The value of the mock fish system is that it not only permits a broad screening of additives, but it also permits one to determine, in efficacy studies, whether microbial inhibition is due to additives alone or partly to substrate antibiotic components such as certain polypeptides (J. T. R. Nickerson pers. commun.). It affords a method of controlling some variables and/or allowing the study of effects upon specific microorganisms. We have employed versions of

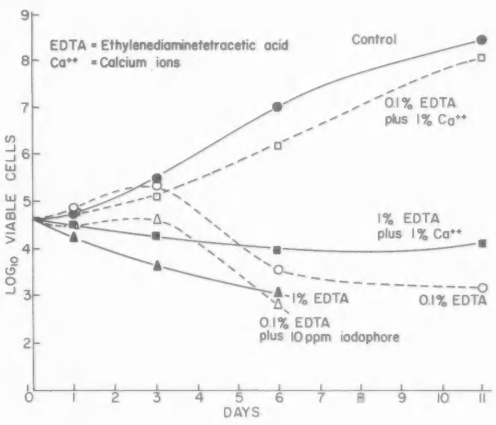

FIGURE 1.—Survival of *Pseudomonas* spp. in mock fish.

mock fish before in irradiation studies in which we either embedded the inoculum evenly throughout the gelatin disc or smeared the same size inoculum on one surface of the gelatin disc (Green and Kaylor 1977). The method might be extended to other applications where some detail or specific effects are to be elucidated.

From Figure 1 it is obvious that 1% calcium ions negate the effect of 0.1% EDTA and reduce the effect of 1% EDTA. An improved effect is noticed when 10 ppm iodophor is coupled with 0.1% EDTA, and this was somewhat expected.

The implied conclusion is that 1% EDTA embedded in ice, free of divalent ions, will reduce the outgrowth of *Pseudomonas* spoilage organisms on iced fish and that the inhibitory effect of 0.1% EDTA combined with 10 ppm iodophor is even greater. The expected results obtained with the mock fish supports their reliability for the intended use, but it is not suggested for use as a substitute for efficacy tests. Therefore, conculsions regarding the effectiveness of inhibitory additives for any specific substrate must ultimately be derived from conventional efficacy tests.

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REPRODUCTIVE CYCLE OF THE PINK SURFPERCH, *ZALEMBIUS ROSACEUS* (EMBIOTOCIDAE)

Embiotocids received early attention from biologists (e.g., Eigenmann 1892) partly because of the viviparous mode of reproduction displayed by fishes of this family. The pink surfperch, *Zalembius rosaceus* (Jordan and Gilbert), is one of the lesser known members of this group. What is most distinctive about *Z. rosaceus* as compared with other embiotocids is the timing of the various events of its annual reproductive cycle. The purpose of this report is to describe this cycle.

Materials and Methods

Specimens were collected off the coast of southern California at depths ranging from 27 to 33 m. Samples were taken from Redondo Beach, Los Angeles County, to San Clemente, Orange County, Calif. Monthly collections were obtained from May 1972 to September 1973 and January and March 1977. Collections were made using otter trawls from the Occidental College RV *Vantuna* and from the RV *Fury II*, operated by the Orange County Board of Education. Specimens from July, August, and September 1973 were provided by the Southern California Coastal Water Research Project. Specimens were also examined in the ichthyology collection of the Los Angeles County Museum of Natural History.

The fish were preserved in 10% Formalin.[1] Gonads were embedded in paraffin. Histological sections were cut at 8 μm and stained with iron hematoxylin followed by eosin counterstain. Gonads were sectioned from the following numbers of females: January (7), February (4), March (11), April (6), May (5), June (10), July (1), August (15), September (18); October (3); December (6); and from 85 males, as shown in Table 1. Sectioned material was collected in 1973 except that for May, June, October, and December 1972.

Results and Discussion

The gonadal morphology and histology of *Z. rosaceus* closely resembles that of the embiotocids *Cymatogaster aggregata* as described by Eigen-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

mann (1892), Turner (1938), and Wiebe (1968) and *Embiotoca jacksoni* by Lagios (1965).

The seasonal testicular cycle is summarized in Table 1. From August to November, testes are regressed with the seminiferous tubules containing mainly spermatogonia and Sertoli cells. Testicular recrudescence (i.e., renewal of the germinal epithelium to start a new cycle) was evident in December. The testicular cycle was far advanced in one December male whose testes contained small clusters of sperm. The major period of spermiogenesis (sperm formation) occurred from March through June (Table 1). Germinal epithelium was exhausted or greatly reduced in seminiferous tubules of regressing testes which were first observed (Table 1) in June males. In these testes, lumina are typically filled with compact sperm cysts called spermatophores by Wiebe (1968). Some breeding may conceivably continue as late as July because residual sperm cysts lingered into this month in the regressing testes of three males. While the exact duration of the mating season is not known for *Z. rosaceus*, the testicular cycle seems to indicate that it encompasses March–June.

Embryos were observed for the first time in ovarian histological sections from 7 of 15 August females. The gestation period appears to last about 5–7 mo as one December and one January female gave birth while in the otter trawl aboard ship, and females that had recently given birth, as well as several that were still gravid, were found in the January and March 1977 samples. The 23 gravid females that were examined contained a mean of 3.5 young (range 2–6). A sample of 26 near-term young that were removed from females during this period averaged 34 mm SL.

There appear to be two trends in the timing of the reproductive cycles of California embiotocids. In the first, breeding occurs mainly during autumn with the young being born in spring and summer. This group includes *Amphistichus argenteus* (Carlisle et al. 1960), *Brachyistius frenatus* (Feder et al. 1974), *Damalichthys vacca* (Feder et al. 1974), *E. jacksoni* (Lagios 1965), *Hyperprosopon argenteum* Rechnitzer and Limbaugh 1952), and *H. ellipticum* (Feder et al. 1974). Young of *D. vacca* may appear as late as October (Feder et al. 1974). In the second group, breeding takes place during the summer with parturition occurring the following spring and summer. This group includes *Amphigonopterus* (= *Micrometrus*) *aurora, Micrometrus minimus* (Hubbs 1921), and *C. aggregata* (Bane and Robinson 1970; Shaw et al. 1974).

The timing of the reproductive cycle of *Z. rosaceus* with mating in the spring and parturition in the winter is a pattern clearly distinct from that currently known for any other California embiotocid. The advantages of this type of cycle are not clear at this time and further studies on the biology of this species will be necessary.

TABLE 1.—Monthly samples of *Zalembius rosaceus* showing percentage of males in various stages of the testicular cycle.

Month	N	Spermiogenesis	Partial regression	Total regression	Recrudescence
Jan.	5	0	0	60	40
Feb.	8	50	0	12	38
Mar.	12	75	0	8	17
Apr.	10	100	0	0	0
May	13	100	0	0	0
June	4	75	25	0	0
July	3	0	100	0	0
Aug.	6	0	0	100	0
Sept.	7	0	0	100	0
Oct.	10	0	0	100	0
Dec.	7	14	0	14	72

Acknowledgments

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GALLBLADDER LESIONS IN CULTURED PACIFIC SALMON

This note records observations on a previously unreported biliary lesion in the gallbladders of various samples of coho, *Oncorhynchus kisutch;* chinook, *O. tshawytscha;* and sockeye, *O. nerka,* salmon cultured mainly in Puget Sound, Wash., during 1974–76. There were no obvious signs of distress or physical debilitation in affected fish. The gallbladders were enlarged and impacted with an amorphous yellow or white material which, in some instances, extended into the common bile duct (Figure 1).

Efforts to prove infectious origin were unsuccessful. No bacteria were consistently isolated from gallbladder or hepatic tissues and attempts to demonstrate a viral agent on a chinook cell line were negative. Possibilities of protozoan or helminth parasitism were discounted after microscopic examination of tissues, gallbladder, and intestinal contents.

Normal and impacted gallbladder, liver, and kidney tissues were fixed in 10% buffered Formalin[1] and stained sections were prepared at Northwest and Alaska Fisheries Center (NWAFC), NMFS, NOAA, Seattle, Wash. Excessive vacuolation of the columnar epithelium was evident in affected gallbladders (Figure 2). No lesions were observed in either the livers or kidneys of fish with the gallbladder condition.

Preliminary studies (Table 1) indicate a predominance of an as yet uncharacterized mucopolysaccharide material in impacted gallbladders. Serum bilirubin, cholesterol, and glucose concentrations of coho salmon with impacted gallbladders were not different from those found in normal fish.

TABLE 1.—Composition of material in impacted gallbladders in coho salmon.

Material	Percentage
Solids (dry wt @ 105°C)	30.4
Ash	14.2
Nitrogen	1.25
Reducing sugar (ortho-toluidine method)	11.52

Case History

Impacted gallbladders were first observed in May 1974, when 25 yearling coho salmon from saltwater pens in southern Puget Sound were referred to the disease laboratory at NWAFC Aquaculture Experiment Station near Manchester, Wash., for diagnosis of an unrelated skin infection (Table 2). The condition was detected in four separate lots of coho and chinook salmon in central Puget Sound during the summer growing season of 1974. In July 1975, the lesion was seen in a subsample of 250 chinook salmon smolts in a private freshwater rearing pond in Oregon (Table 2). Several lots of salmon being held for husbandry and disease research at the Aquaculture Experiment Station have also been found to have this condition.

Four thousand 0-age coho salmon smolts (18–20 g) reared on commercially prepared Oregon Moist Pellets (OMP) were transferred to saltwater pens at the Aquaculture Experiment Station in early August 1976 where they continued to receive the same ration. Smolts of the same stock (1,000) were

[1]Reference to trade names does not imply endorsement of the National Marine Fisheries Service, NOAA.

FIGURE 1.—Impacted material can be clearly seen in the gallbladder of affected coho salmon (upper fish). Normal gallbladder (lower fish) is shown for comparison.

TABLE 2.—Occurrence of impacted gallbaldders in Pacific salmon subsampled from saltwater and freshwater rearing areas.

Date	Species	Age	Feed	No. of fish in lot	No. of fish examined	Percentage of fish examined with gallbladder anomalies	Environment and site
May 1974	Coho	1+	OMP[1]	—	25	100	Net pens: South Puget Sound
Oct. 1974	Coho	1+	OMP	100,000	100	90	Net pen: Central Puget Sound
Oct. 1974	Coho	1+	OMP	100,000	100	76	Net pen: Central Puget Sound
Oct. 1974	Coho	1+	OMP	100,000	165	90	Net pen: Central Puget Sound
Oct. 1974	Chinook	0+	OMP	100,000	157	89	Net pen: Central Puget Sound
July 1975	Chinook	0+	OMP	50,000	250	90	Freshwater holding pond: lower Columbia River
Aug. 1975	Sockeye	1+	OMP	450	39	85	Net pen: Research fish, Manchester, Wash.
Sept. 1975	Coho	1+	OMP	250	160	93	Net pen: Research fish, Manchester
Nov. 1975	Coho	1+	OMP	164	164	85	Net pen: Research fish, Manchester
Nov. 1975	Coho	1+	Dry[2]	9,000	600	0	Net pen: Central Puget Sound
Dec. 1975	Chinook	2+	OMP	40	40	0	Cultured brood stock: Manchester
Dec. 1975	Coho	2+	OMP	94	94	0	Cultured brook stock: Manchester
Dec. 1975	Coho	3	Natural	25	25	0	Mature fish returning from sea: Manchester
Dec. 1975	Coho	1+	OMP	500	200	0	Freshwater station: Seattle, Wash.
Jan. 1976	Coho	1+	SC[3]	400	40	0	Freshwater station: Seattle
Jan. 1976	Coho	1+	OMP	66,000	60	99	Net pen: Research fish, Manchester
Oct. 1976	Coho	1+	OMP	1,600	120	75	Net pen: Research fish, Manchester
Oct. 1976	Coho	0+	OMP	1,000	100	0	Freshwater station: Seattle
Oct. 1976	Coho	0+	OMP	4,000	180	38	Net pen: Research fish, Manchester
Aug.–Oct. 1976	Coho	1+	Dry	100,000+	114	37	Net pen[4]: Central Puget Sound

[1]Oregon Moist Pellet — Commercial product.
[2]Commercial dry pelleted ration.
[3]Fish fed experimental OMP diet containing single cell protein.
[4]Pers. commun., D. Weaver, Domsea Farms, Gorst, Wash.

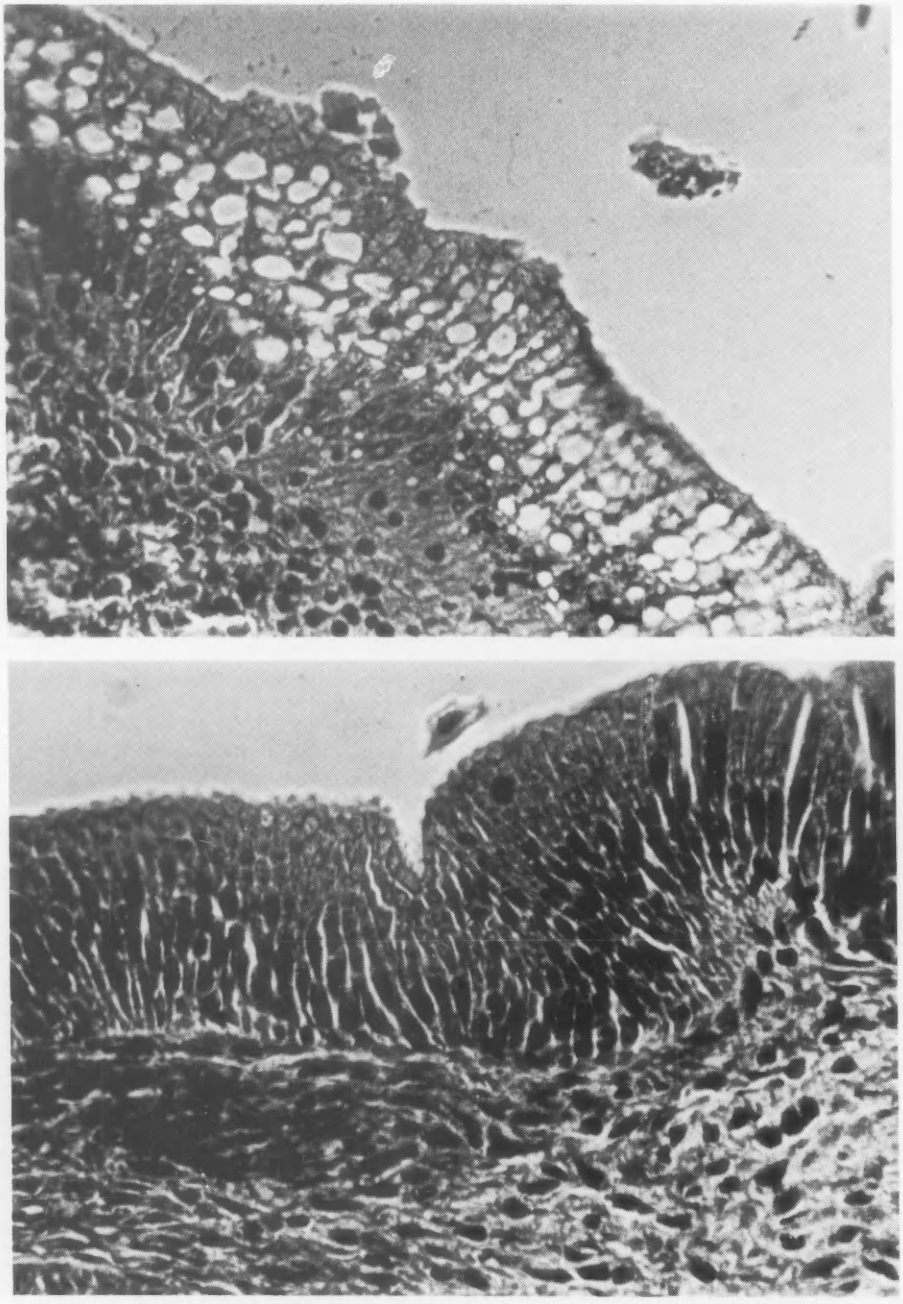

FIGURE 2.—Upper photo shows histopathologic features (vacuolation) of the epithelium from an impacted gallbladder of a small coho salmon cultured in saltwater. Lower photo shows normal epithelium of the gallbladder from a small wild coho salmon collected in saltwater. Hematoxylin-eosin stain; ×320.

held back for freshwater rearing. Approximately 38% of the fish in saltwater were found to have the gallbladder condition by mid-October. The condition did not develop in those remaining in freshwater.

In all cases observed thus far, affected fish were young (<2 yr) salmon that had been reared exclusively on commercially prepared pellets. With the exception of the occurrence in Oregon, all cases of the abnormality have occurred in saltwater net pens.

With dietary adjustments the condition is apparently reversible. In an unrelated nutrition study, 75% of the subsamples of one lot of 1,800 coho salmon that had been fed a ration of OMP for several months had impacted gallbladders. These test fish were divided into two lots. One group (1,400) was fed a laboratory prepared moist pellet diet and the remaining fish (400) were continued on the commercial OMP diet. After 4 mo, subsamples indicated that incidence of abnormal gallbladders in fish on the laboratory diet had been reduced to 5%. Incidence of the condition in the test group maintained on the OMP diet remained at 75%.

Discussion

I have found no published information relative to gallbladder abnormalities in fishes. The pathological features described for this condition do not resemble any infectious disease currently described for fishes and are more suggestive of a toxic or nutritional disorder.

The biliary system is an integral part of the digestive apparatus, playing an important role in lipid digestion. It also provides a mechanism for recycling certain metabolic byproducts of hepatic origin through the digestive system. Many of these metabolic byproducts are excretory wastes while others can be salvaged for reuse by redigestion. Studies as yet do not prove a major detrimental effect of this condition on the fish. Knowing the importance of the biliary system, however, it is inconceivable that it does not have an adverse effect on the animals' nutritional status, particularly in relation to systems dependent upon adequate and diverse lipid supply.

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TIMING OF THE SURFACE-TO-BENTHIC MIGRATION IN JUVENILE ROCKFISH, *SEBASTES DIPLOPROA*, OFF SOUTHERN CALIFORNIA

Species of the genus *Sebastes* lead a pelagic existence as larvae, transforming to pelagic prejuveniles and finally benthic juvenile stages at varying sizes (Moser 1967, 1972). Pelagic prejuveniles of some species often congregate under drifting objects (Hitz 1961); off the coast of southern California, *Sebastes diploproa* (Gilbert 1890) is the dominant rockfish species found under drifting kelp (Mitchell and Hunter 1970). Adults of this species inhabit a bathymetric range of 91–578 m and a latitudinal range from Alaska to Baja California (Hart 1973). Little is known about the movement of this rockfish from surface to benthic waters. This paper provides information on the disappearance from surface waters and the appearance in the benthic habitat based on seasonal size distribution from the two habitats.

Materials and Methods

Surface prejuveniles were collected by dip net off San Diego, Calif. (lat. 32°52′N, long. 117°30′W), from beneath drifting kelp (primarily *Macrocystis pyrifera*) during 1975 and 1976. Benthic juveniles were sampled in standard 10-min bottom trawls with a 7.6-m (25-ft) otter trawl (12.7-mm stretch mesh cod end liner) in 1972 through 1976. Most trawls were made in and around the Los Angeles Bight from Point Dume (lat. 34°00′N, long. 118°48′W) to Dana Point (lat. 33°28′N, long. 117°43′W) at depths from 92 to 183 m, although small *S. diploproa* were captured as shallow as 46 m. This does not encompass the entire adult bathymetric range, but younger stages of *Sebastes* generally tend to occupy shallower parts of the adult range (Kelly and Barker 1961; Moser 1967, 1972; Westrheim 1970). Only

those trawls containing one or more specimens of *S. diploproa* were considered, a total of 96 trawls.

Results

Surface dip net collections consisted of 873 prejuveniles, the largest of which was 58.7 mm standard length (SL). A total of 2,418 benthic juveniles were taken in the trawl collections, with the following size breakdown: <30mm, 2; 30–39 mm, 84; 40–49 mm, 892; and 50–59 mm, 1,440. Few prejuveniles larger than 50 mm SL were captured in surface collections (Figure 1); thus they appear to settle out at a size under 50 mm. At this size prejuveniles are about 1 yr old according to laboratory growth measurements (unpublished data) and the growth curve determined by Phillips (1964); this is well within the range of published values for other members of the genus. Age of settlement has been estimated to be 6 mo for *S. umbrosus* (Chen 1971), 4 or 5 mo for *S. marinus* (Kelly and Barker 1961), and 6-12 mo for *S. alutus* (Westrheim 1973; Carlson and Haight 1976).

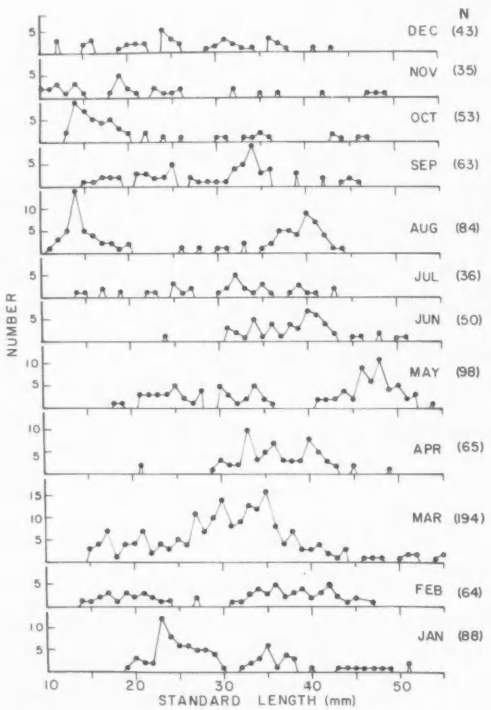

FIGURE 1.—Monthly size distribution for surface prejuvenile *Sebastes diploproa* from the combined dip net collections of 1975–76. Parenthetical numbers indicate numbers of fish collected in that month.

Female *S. diploproa* are ovoviviparous, releasing yolk sac larvae from February to July off California (Phillips 1964). The abundance of newly transformed prejuveniles (10–14 mm SL) in August through December indicates that the principal parturition season occurred in the latter part of this interval (Figure 1). The presence of small individuals in February and March, however, may indicate that there were two principal parturition seasons. Westrheim (1975) provided evidence for two parturition seasons in 1973 off British Columbia (July and October–December) and suggested that this species might release larvae throughout the year.

Surface prejuveniles in the correct size category for settlement were present throughout the year but their abundance was greatest in late spring to early summer. The percentage of specimens larger than 40 mm SL peaked in May and dropped off rapidly thereafter (Figure 2), suggesting that emigration from surface waters occurred primarily in May and June. For comparison, seasonal abundance of pelagic prejuveniles of three other *Sebastes* species are shown (Figure 3). Emigration from surface waters occurred in January to February for *S. rubrivinctus*, May to June for *S. paucispinis*, and July to August for *S. serriceps*.

Benthic juvenile *S. diploproa* occurred in a highly clumped distribution (variance exceeded mean number of fish per trawl for all months with more than one trawl). Since several months were undersampled or lacked a sufficient number of trawls, data were combined by 2-mo intervals (Figure 4). Small benthic juveniles first appeared in July–August; abundance peaked in November–December and tapered off thereafter.

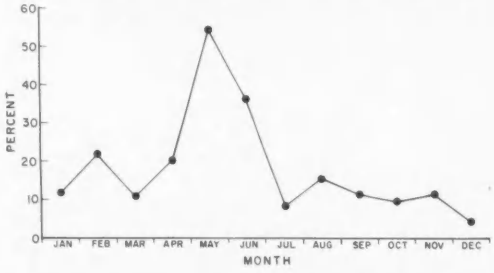

FIGURE 2.—Percentage of surface prejuvenile *Sebastes diploproa* >40 mm SL from the combined dip net collections of 1975–76.

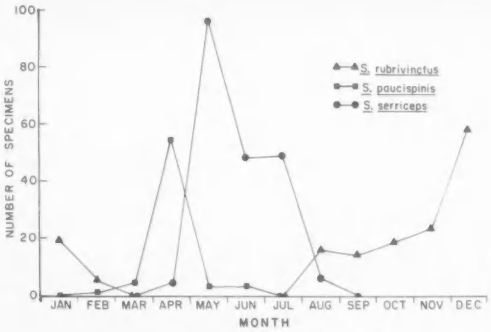

FIGURE 3.—Monthly abundance of surface prejuveniles of *Sebastes rubrivinctus*, *S. paucispinis*, and *S. serriceps* from the combined dip net collections of 1975–76.

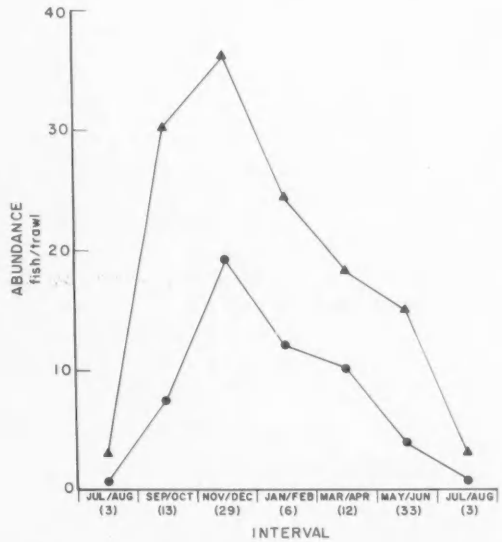

FIGURE 4.—Bimonthly abundance (number caught per trawl) of benthic juvenile *Sebastes diploproa* from trawl collections of 1972 through 1976. Circles represent abundance of all specimens <50 mm; triangles, all <60 mm. Parenthetical numbers indicate the number of trawls made per interval.

Discussion

Surface size distribution and abundance data indicate that the bulk of emigration from the surface occurred in late spring to early summer (Figures 1, 2), whereas appearance of benthic juveniles began in midsummer and continued over a period of several months (Figure 4). The temporal discrepancy between disappearance from the surface and peak benthic appearance suggests that migrant juveniles may occupy an intermediate habitat between emigration and settlement. During this period, the juveniles are probably in midwater, as shown for *S. macdonaldi* by Moser (1972). Four specimens of *S. diploproa* have been taken in two discrete-depth midwater trawls by the RV *Velero IV* and are presently in the fish collection of the Natural History Museum of Los Angeles County (LACM). Three of these specimens (43, 47, 48 mm SL) were captured in October 1970 at a depth of 250 m off San Clemente Island (lat. 32°39′N, long. 118°11′W; LACM 36315-1); the fourth specimen (43 mm SL) was taken in December 1970 at a depth of 200 m off Santa Catalina Island (lat. 33°21′N, long. 118°46′W; LACM 36307-1). Both tows were taken between 0200 and 0430 (local time) over bottom depths of 1,915 and 1,280 m, respectively. Since these bottom depths greatly exceed the bathymetric range for *S. diploproa*, time may be spent in horizontal movement to benthic habitat of suitable depth. Early migrants may come from nearshore areas, such as those sampled in the dip net collections, whereas those appearing later in the year may come from offshore prejuvenile populations; larval *Sebastes* are known to be distributed hundreds of kilometers offshore (Ahlstrom 1961).

Southern California is near the southern end of the geographic range for *S. diploproa* (Phillips 1964); no information was available on the surface prejuveniles of this species from the center or northern parts of its range. Extension of the timing of emigration and subsequent appearance in the benthic habitat is probably a direct result of the long parturition season off California. Westrheim (1975) has shown that two parturition seasons may occur per year off British Columbia and has suggested that limited year-round spawning may take place. In general, however, as one goes further north, the principal parturition season is progressively shorter and later; off Oregon, the season is mid-May to June (Hitz 1962), June to July off Washington (DeLacy et al. 1964), and July off British Columbia (Westrheim 1975). I would expect surface prejuvenile year classes to be more distinct in the north than shown in my data (Figure 1), and that timing of emigration from surface waters would be more precise.

Acknowledgments

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